VOL. 25, NO. 2 E&A NOVEMBER 1956

THE JOURNAL OF ANIMAL ECOLOGY

COMMONWEALTH INST. OF ENTOMOLOGY LIBRARY
24 MAR 1958
SERIAL Eu.431
SEPARATE

EDITED FOR THE

BRITISH ECOLOGICAL SOCIETY

BY

H. C. GILSON

BLACKWELL SCIENTIFIC PUBLICATIONS · OXFORD

CHARLES C THOMAS · PUBLISHER
SPRINGFIELD ILLINOIS

THE RYERSON PRESS
TORONTO CANADA

ANNUAL SUBSCRIPTION: FORTY-FIVE SHILLINGS (U.S.A. $7.50)
SINGLE NUMBERS: TWENTY-NINE SHILLINGS (U.S.A. $4.75)

THE JOURNAL OF ECOLOGY

VOL. 44 NO. 2 EDITOR: H. GODWIN JULY 1956

CONTENTS

Ecology of *Alnus glutinosa* (L.) Gaertn. V. Note on some British alder populations. By D. N. McVEAN.

Ecology of *Alnus glutinosa* (L.) Gaertn. VI. Post-glacial history. By D. N. McVEAN.

Preliminary investigation of factors determining the growth form on *Cerastium tetrandum* Curt. By F. WHITEHEAD.

The vegetation of the Imatong mountains, Sudan. By J. K. JACKSON.

On the chemical composition of some waters from the Moor House Nature Reserve. By E. GORHAM.

Some preliminary observations on the ecology of pit heaps. By J. K. BRIERLEY.

An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks. By G. C. EVANS.

Ecology of the Pembrokeshire islands. V. Manuring by the colonial seabirds and mammals, with a note on seed distribution by gulls. By M. E. GILLHAM.

The ecology of Woodwalton Fen. By M. E. D. POORE.

Two blanket-bogs in Sutherland. By W. H. PEARSALL.

Succession of fungi on decaying cocksfoot culms. Part I. By J. WEBSTER.

The vegetation of Upper Teesdale in the North Pennines. By C. D. PIGOTT.

Mercurialis perennis L. in Ireland. By D. J. BOATMAN.

Studies of the development of woodland conditions under different trees. V. The mineral composition of the ground flora. By J. D. OVINGTON.

The nature and origin of the soils over the Cornish serpentine. By D. E. COOMBE and L. C. FROST.

Reviews: British Ecological Society (Notes of Meetings, Constitution and Rules, Accounts, List of Members): Biological Flora of the British Isles.

Articles are illustrated with plates and text-figures

Beginning with Vol. 45 *each volume will consist of three parts, the subscription price of which will be* 84s. *net, per volume; single parts will remain at* 35s. *net.*

BLACKWELL SCIENTIFIC PUBLICATIONS

THE FAUNA AND BIOMASS OF A MUDDY SAND DEPOSIT OFF PORT ERIN, ISLE OF MAN

By N. S. JONES

Marine Biological Station, Port Erin

WITH AN APPENDIX ON METHODS USED FOR THE ANALYSIS OF DEPOSITS

By D. J. Slinn

Marine Biological Station, Port Erin

(With 6 Figures in the Text)

CONTENTS

	PAGE
Introduction	217
Methods	219
Environmental Conditions	219
Seasonal Samples	220
Comparative Samples	224
The Muddy Sand Fauna as a Community	237
The Role of Fish in the Community ...	239
Data on Life-histories and Growth ...	241
Conclusions	246
Acknowledgments	247
Summary	247
Appendix: Methods Used for the Analysis of Deposits and Animal Material ...	247
References	251

INTRODUCTION

The bottom fauna in the open sea seems to be fairly stable in composition both qualitatively and quantitatively, yet the species and numbers of animals present vary considerably from place to place and often within short distances. In a relatively small area such as the northern Irish Sea most of the environmental conditions away from the influence of rivers are uniform within narrow limits, and such variations as occur for example in the temperature and salinity of the water are not great enough to cause the differentiation into assemblages or communities observed in the fauna; nor do they change sufficiently from year to year to cause much alteration in the total numbers or weights of animals in a single locality. Harvey (1950) comments on the variation in population densities of filter-feeding organisms over adjacent areas where there is no reason to suppose that there is any marked difference in the food supply. The most obvious variant in the environment is the physical composition of the sea bottom, and it is the physiological and morphological organization peculiar to each species that seems to determine the range of deposits upon which it will survive or, where applicable, settle. Such a process will inevitably cause differentiation into communities, provided that there is some discontinuity between a few types of deposit, and since some grades of deposit seem to be more favourable than others there will also be variations in the numbers of species present from place to place.

Differences in the weight of animals or biomass between different places may be due to differences in numbers of species and also to differences in the size and life-histories of the species in each locality. Large species will naturally have a larger mass than smaller ones, but this may be counteracted by greater reproductive potential among the small species, resulting in their presence in larger numbers. The biomass at any one time on a given deposit must depend on many interacting factors and processes; nevertheless it is possible that there are factors which set a limit to the potential biomass regardless of variations in the composition of the

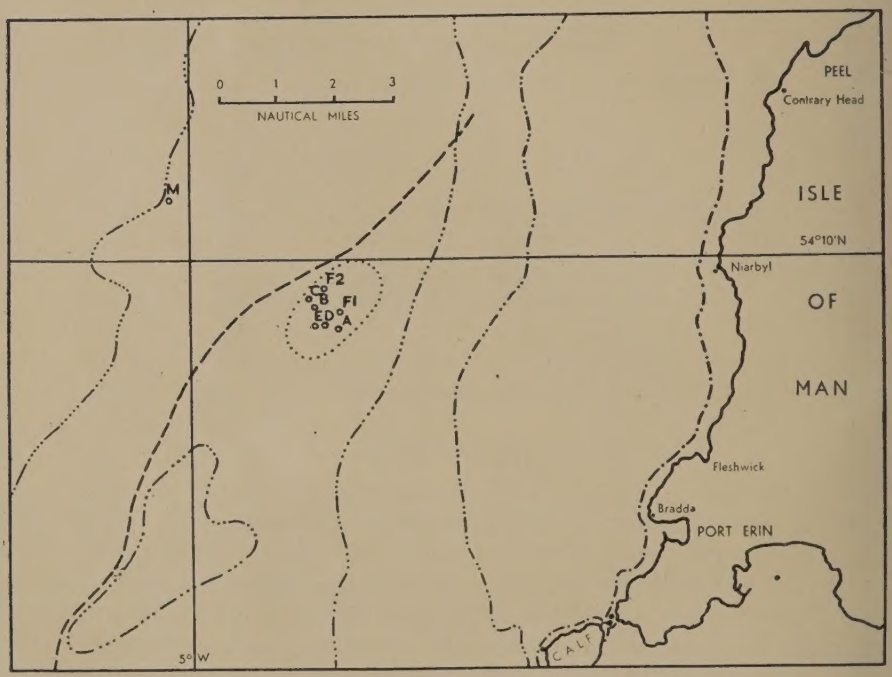


Fig. 1. Map of the area off the south-west coast of the Isle of Man, showing positions of stations: . . . . . , boundary of selected muddy sand area; — — — —, approximate boundary between muddy sand and mud; — · —, 10 fm; — · · —, 20 fm; — · · · —, 30 fm; — · · · · · —, 50 fm.

fauna. Provided that such a limit exists and is approached there are three methods of testing the possibly limiting factors: by comparing the biomass at different localities with the same grade of deposit, by comparing the biomass at a single locality at intervals over a period of years and by experiment. Although it is possible that other unknown factors presumably chemical are involved, the factor that appears most likely to be limiting in this respect is the concentration of nutrient salts, especially phosphates, dissolved in the overlying water. All animal life in the sea is ultimately dependent on the presence of plants, and of these the phytoplankton is by far the most important.

The first method is unlikely to show positive results since it is difficult to find two or more places where the phosphate content of the water differs sufficiently while other environmental factors are approximately uniform. The second method is more likely to be successful provided that the right place is chosen, for success depends upon a change in phosphate concentration. There is some evidence that such a change may have an influence on the quantity of fish present in one area as Cooper (1948*b*) has shown for dogfish off Plymouth, and there are good reasons for assuming that phosphate may be limiting for the zooplankton (Harvey 1950, Armstrong & Harvey 1950). The experimental method has been used by Gross, Raymont and others in a partially enclosed sea loch, but it is probably impracticable in the open sea; however, their results show that phosphate concentration does affect the benthos (Raymont 1950), and it is possible that laboratory experiments might provide detailed proof at least for certain species. This paper is mainly the result of an attempt to investigate the possibilities of the first method and to provide basic data for the second. The muddy sand area was chosen because the fauna is comparatively rich and the deposit is suitable for reliable sampling.

Table 1. *Percentage of each grade in deposit samples*

	Gravel	Coarse sand				Fine sand	Silt & clay
Particle size (mm)	2	2-1·0	1·0-0·5	0·5-0·25	0·25-0·20	0·20-0·0313	0·0313
Sample	(1)	(2)	(3)	(4)	(5)	(6)	(7)
F1	0·4	0·1	49·2	38·4	6·7	3·0	2·1
F2	0·1	0·2	9·4	36·2	22·4	18·4	13·2
S1	0·4	0·3	4·3	15·3	39·5	20·5	19·7
M	—	—	3·9	4·1	14·0	43·5	34·6

METHODS

The main series of samples were taken with a 0·1 m^2 van Veen bottom sampler. Additional hauls were obtained using a runner-dredge with a stramin bag to sample the more active animals in the benthos and those living close to the bottom. Bottom samples were washed through a sieve with 2 mm diameter circular holes and the animals retained were preserved for later examination in 5% formalin in sea water. The contents of the dredge were brought back to the laboratory unsorted and examined a portion at a time. For chemical and mechanical analyses of the deposit the total contents of a grab haul were thoroughly mixed, and portions of this were dried in an oven at 105° C until no further loss of weight occurred and then stored in sealed bottles. Deposit samples were mechanically graded as described by Holme (1953) except that the 0·125 mm sieve was omitted from the series.

ENVIRONMENTAL CONDITIONS

The area selected for the main survey was roughly 2 miles in length from S-W to N-E and 1 mile in width, centred 6½ miles on a bearing 304° from Bradda Head (Fig. 1), the depth increasing seawards from 32 to 39 fathoms. The whole of the

area may be classed as muddy sand, but within the fairly small depth range included the deposit varies appreciably, becoming softer with a greater proportion of mud as the depth increases. At the outer edge of the selected area the deposit rapidly changes into a sticky mud. A series of samples (S) was taken off the Cumberland coast for comparison with the main series in a position mid-way between Stations 49 and 55 of May 1950 (Jones 1952, Fig. 1). The deposit in this case consisted of muddy sand at a depth of 10 fm. Some mechanical analyses of deposit samples from the main area and outside it are given in Table 1.

Some figures showing salinities and temperatures for the two areas are given in Jones (1951, 1952). Salinity is somewhat lower off the Cumberland coast, the mean value at the surface being 32·5‰ compared with 34·2‰ off Port Erin. The temperature range is somewhat greater off the Cumberland coast than off Port Erin, but the differences are not large enough to be likely to cause any significant differences in the composition of the benthos.

SEASONAL SAMPLES

Five series (A, B, C, D and E) each of ten 0·1 m^2 samples were taken during 1952 at intervals of 2-3 months. Results are shown in Table 2. There is no distinct variation in total numbers of individuals or wet weights of animals in the bottom samples that can be attributed to seasonal changes. There are some differences apparent between series but these are probably due mainly to differences in location. It was not possible in the circumstances to take each series in exactly the same place, and it was not considered advisable to attempt to mark the area with buoys as there would be little chance of their remaining in position over a long period, so that owing to poor visibility on some occasions position had to be fixed by dead reckoning. The difference in position was not thought to be greater than $\frac{1}{2}$ mile between any of the series, but this is sufficient to show considerable changes in the fauna. Series A, D and E are probably all representative of a similar bottom and were taken within an area and depth range (32-36 fm) small enough to be fairly uniform, but Series C, taken on 4 June, probably represents a fauna transitional towards the mud ground lying outside and in deeper water than the muddy sand. It was taken in a somewhat greater depth than the others (37-39 fm) and the bottom deposit brought up was somewhat more muddy. This is reflected in the numbers of certain species present, and is obviously significant in the case of *Corbula gibba*, of which only one individual was obtained in Series C while the numbers in Series A, D and E were respectively 274, 264 and 241. Series B, taken on 15 April, was probably transitional between the faunas represented in A, D and E on the one hand and C on the other. This is borne out by the numbers of *Corbula* in each bottom sample (Table 3). The total numbers in the series are considerably lower (126) than in A, D or E and it is evident that the numbers per haul are more inconsistent. The total numbers and wet weight of animals in Series C were a good deal lower (162 and 43·6 g/m^2) than in Series A, D and E, in which there were 506, 937 and 780 individuals and 55·5, 97·3 and 74·4 g/m^2, with a

Table 2. *Numbers and occurrence of all species in seasonal samples on muddy sand ground off Port Erin, 1952*

Series (each 10 samples 0·1 m²)	A		B		C		D		E		Total	
Date (1952):	20 Feb.		15 Apr.		4 June		30 Sept.		23 Dec.			
Depth (fm):	32-34		33-37		37-39		34-36		36			
	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.
FORAMINIFERA												
Astrorhiza limicola Sandahl	—	—	—	—	—	—	11	5	109	10	120	15
COELENTERATA												
Thecocarpus myriophyllum (L.)	1	1	1	1	—	—	—	—	1	1	5	4
Cerianthus lloydi Gosse	—	—	—	—	—	—	1	1	—	—	1	1
PLATYHELMINTHES												
Leptoplana tremellaris (O. F. Müller)	3	2	1	1	—	—	1	1	—	—	5	4
NEMERTINEA												
Amphiporus sp.	2	2	4	4	1	1	5	5	7	6	19	18
POLYCHAETA												
Aphrodite aculeata L.	1	1	—	—	—	—	2	2	—	—	3	3
Harmothoe sp.	3	1	3	3	—	—	—	—	—	—	6	4
Harmothoe longisetis (Grube)	—	—	—	—	—	—	—	—	1	1	1	1
H. antilopis McIntosh	—	—	—	—	—	—	1	1	2	2	3	3
H. lunulata (Delle Chiaje)	2	2	1	1	—	—	—	—	—	—	3	3
Lagisca extenuata (Grube)	—	—	—	—	—	—	—	—	1	1	1	1
Eulalia sp.	1	1	—	—	—	—	—	—	—	—	1	1
Eulalia sanguinea Oersted	—	—	—	—	—	—	—	—	2	2	2	2
Ophiodromus flexuosus Delle Chiaje	—	—	2	2	—	—	—	—	—	—	2	2
Nephthys incisa Malmgren	16	9	24	10	22	9	19	9	10	7	91	44
Glycera gigantea Quatrefages	—	—	—	—	—	—	—	—	1	1	1	1
G. rouxi Aud. & M.-Edw.	4	4	4	4	11	7	6	5	3	3	28	23
Goniada maculata Oersted	16	10	9	5	1	1	6	4	9	5	41	25
G. norvegica Oersted	1	1	—	—	—	—	—	—	—	—	1	1
Eone nordmanni Malmgren	—	—	—	—	—	—	2	2	3	3	5	5
Eunice harrassi Aud. & M.-Edw.	—	—	—	—	—	—	—	—	1	1	1	1
Onuphis conchylega Sars	—	—	—	—	—	—	—	—	3	3	3	3
Lumbriconereis spp.	9	7	8	5	4	3	12	8	10	9	41	32
Notocirrus scoticus McIntosh	3	3	1	1	—	—	5	5	4	3	13	12
Laonice cirrata (Sars)	—	—	—	—	—	—	9	4	11	8	20	12
Spio filicornis (O. F. Müller)	—	—	1	1	—	—	1	1	1	1	3	3
Spiophanes bombyx (Claparède)	—	—	—	—	1	1	8	7	—	—	9	8
Prionospio spp.	13	4	6	3	3	3	4	3	8	5	34	18
Polydora flava Claparède	—	—	—	—	—	—	1	1	—	—	1	1
Poecilochaetus serpens Allen	—	—	—	—	—	—	1	1	—	—	1	1
Chaetozone setosa Malmgren	4	2	—	—	—	—	11	6	11	7	26	15
Diplocirrus glaucus Haase	—	—	1	1	4	4	1	1	7	6	13	12
Scalibregma inflatum Rathke	—	—	—	—	1	1	—	—	—	—	1	1
Ammotrypane cylindricaudatus Hansen	2	2	1	1	—	—	—	—	—	—	3	3
Notomastus latericeus Sars	—	—	3	3	8	6	1	1	—	—	12	10
Clymene gracilis (Sars)	—	—	—	—	—	—	—	—	1	1	1	1
Owenia fusiformis Delle Chiaje	2	2	—	—	3	1	42	10	56	10	103	23
Myriochele heeri Malmgren	—	—	—	—	—	—	4	4	42	9	46	13
Pectinaria spp.	23	7	24	7	9	6	30	7	16	6	102	33
Amphicteis gunneri (Sars)	—	—	—	—	2	2	9	6	15	8	26	16
Amphitrite gracilis (Grube)	—	—	1	1	—	—	—	—	1	1	2	2
Lanice conchilega (Pallas)	—	—	—	—	—	—	2	2	1	1	3	3
Thelepus cincinnatus (Fabricius)	1	1	—	—	—	—	—	—	2	2	3	3
Polycirrus spp.	—	—	—	—	—	—	5	4	—	—	5	4
Trichobranchus glacialis Malmgr.	5	3	5	5	1	1	12	5	8	8	31	22
Terebellides stroemi Sars	3	3	2	2	—	—	6	6	6	4	17	15
Hydroides norvegica Gunnerus	—	—	—	—	—	—	—	—	1	1	1	1

Series:	A		B		C		D		E		Total	
	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.
GEPHYREA												
Phascolosoma elongatum Keferstein	1	1	1	1	1	1	2	2	—	—	5	5
P. procerum Möbius	1	1	—	—	—	—	—	—	1	1	2	2
Phascolion strombi (Montagu)	3	2	—	—	—	—	—	—	2	1	5	3
PHORONIDEA												
Phoronis mulleri de Selys Longchamps	4	2	8	4	9	7	34	8	27	10	82	31
CRUSTACEA												
Iphinoe serrata Norman	1	1	—	—	—	—	6	4	2	2	9	7
Diastylis lucifera (Kröyer)	—	—	—	—	—	—	3	3	—	—	3	3
Leptognathia gracilis (Kröyer)	—	—	—	—	—	—	—	—	5	3	5	3
L. brevimana (Lilljeborg)	—	—	—	—	—	—	—	—	3	3	3	3
Cirolana borealis Lilljeborg	1	1	2	2	—	—	3	2	2	2	8	7
Hippomedon denticulatus (Bate)	—	—	—	—	—	—	3	3	2	2	5	5
Ampelisca spp. juv.	—	—	3	3	10	4	8	6	1	1	22	14
Ampelisca spinipes Boeck	7	5	—	—	2	2	2	2	4	3	15	12
A. tenuicornis Lilljeborg	—	—	—	—	—	—	1	1	7	5	8	6
Harpinia antennaria Meinert	—	—	1	1	—	—	—	—	—	—	1	1
H. pectinata Sars	1	1	2	2	—	—	3	3	15	7	21	13
H. crenulata Boeck	—	—	—	—	—	—	1	1	—	—	1	1
Epimeria cornigera (Fabricius)	1	1	—	—	—	—	—	—	—	—	1	1
Cheirocratus intermedius (Sars)	—	—	2	2	—	—	1	1	—	—	3	3
Phtisica marina Slabber	—	—	1	1	—	—	—	—	—	—	1	1
Processa canaliculata Leach	—	—	—	—	—	—	1	1	—	—	1	1
Alphaeus ruber M.-Edw.	1	1	—	—	1	1	2	2	1	1	5	5
Nephrops norvegicus L.	—	—	1	1	1	1	—	—	—	—	2	2
Anapagurus laevis (Thompson)	1	1	1	1	1	1	2	2	1	1	6	6
MOLLUSCA												
Proneomenia aglaopheniae Kovalevsky & Marion	1	1	—	—	—	—	—	—	—	—	1	1
Chaetoderma nitidulum Lovèn	—	—	1	1	—	—	3	3	4	2	8	6
Nucula sulcata Bronn	1	1	19	8	2	2	9	6	10	5	41	22
Lima subauriculata (Montagu)	4	4	—	—	—	—	—	—	4	4	8	8
Thyasira flexuosa (Montagu)	—	—	—	—	—	—	1	1	—	—	1	1
Myrtea spinifera (Montagu)	2	2	—	—	—	—	—	—	1	1	3	3
Cardium ovale Sowerby	—	—	—	—	—	—	—	—	1	1	1	1
C. scabrum Philippi	8	5	22	5	—	—	5	3	6	6	41	19
Dosinia lupinus (Montagu)	6	5	—	—	1	1	6	5	4	3	17	14
Venus striatula (da Costa)	1	1	1	1	—	—	1	1	—	—	3	3
Mysia undata (Pennant)	4	3	2	2	—	—	1	1	1	1	8	7
Abra prismatica (Montagu)	17	7	53	8	40	7	108	10	69	10	297	42
Gari fervensis (Gmelin)	—	—	—	—	—	—	1	1	—	—	1	1
Solecurtus chamasolen (da Costa)	3	3	9	7	1	1	2	2	—	—	15	13
Cultellus pellucidus (Pennant)	15	6	12	8	2	2	19	9	8	5	56	30
Spisula elliptica (Brown)	—	—	—	—	—	—	4	2	2	2	6	4
Corbula gibba (Olivi)	274	10	126	9	1	1	264	10	241	10	906	40
Hiatella arctica (L.)	—	—	—	—	1	1	—	—	1	1	2	2
Thracia phaseolina (Lamarck)	—	—	—	—	—	—	2	1	3	2	5	3
Calopodium pinna (Montagu)	—	—	1	1	—	—	2	2	2	2	5	5
Cuspidaria costellata (Deshayes)	—	—	—	—	—	—	—	—	1	1	1	1
Dentalium entalis L.	6	5	1	1	—	—	4	3	4	4	15	13
Turritella communis Risso	7	6	11	3	7	5	28	5	6	4	59	23
Aporrhais pes-pelicani da Costa	1	1	3	3	—	—	2	1	4	4	10	9
Natica poliana Forbes	2	2	1	1	—	—	—	—	—	—	3	3
Mangelia brachystoma Philippi	—	—	1	1	—	—	—	—	—	—	1	1
Acteon tornatilis (L.)	2	2	—	—	—	—	—	—	—	—	2	2
Cylichna cylindracea (Pennant)	1	1	—	—	—	—	—	—	—	—	1	1
Hermania catena (Montagu)	—	—	—	—	—	—	—	—	3	3	3	3
ECHINODERMATA												
Amphipholis squamata (Delle Chiaje)	—	—	—	—	—	—	—	—	7	5	7	5
Ophiura albida Forbes	—	—	—	—	1	1	2	1	—	—	3	2

Series:	A		B		C		D		E		Total	
	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.
O. affinis Lütken	—	—	2	1	1	1	—	—	—	—	3	2
Amphiura filiformis (O. F. Müller)	—	—	2	2	—	—	32	8	8	6	42	16
A. chiajei Forbes	4	4	4	3	4	3	6	4	9	3	27	17
Echinocardium flavescens (O. F. Müller)	1	1	—	—	—	—	—	—	1	1	2	2
E. flavescens juv.	11	8	3	2	—	—	144	10	44	9	202	29
Brissopsis lyrifera (Forbes)	4	3	—	—	5	4	1	1	1	1	11	9
Echinocyamus pusillus (O. F. Müller)	—	—	2	1	—	—	2	2	11	6	15	9
Leptosynapta inhaerens (O. F. Müller)	3	3	1	1	—	—	5	5	1	1	10	10
Labidoplax buski (McIntosh)	—	—	—	—	—	—	1	1	4	4	5	5
Total individuals	506		398		162		937		780			
Total wet weight (g)	54·49		60·76		43·59		97·28		74·43			

mean of 741 and 75·3 g/m². Among the species identified there is no difference in numbers throughout Series A, D and E that could safely be attributed to anything but sampling errors.

The runner-dredge hauls (Table 4), which were taken over approximately the same period as the bottom samples, besides taking most of the species found in the latter, took a number of the more active animals living close to the bottom. Since the hauls are not strictly comparable no conclusion can be drawn regarding seasonal variation in numbers; however, in the case of some of the lamellibranchs,

Table 3. *Numbers of* Corbula gibba *per sample in 1952 and 1953*

Sample Number	Series A	B	D	E	F1
1	35	11	20	47	79
2	35	34	39	4	57
3	47	24	35	23	62
4	7	20	10	20	45
5	27	11	39	28	42
6	19	11	40	10	43
7	33	6	19	41	90
8	19	—	32	29	33
9	11	7	10	22	55
10	41	2	20	17	20
Total	274	126	264	241	526

of which fairly large numbers were caught, there was some evidence that many young individuals were present during part of the year and that the numbers decreased later. This is borne out by the analysis of certain species on p. 224. It is improbable that this variation makes much difference to the total biomass, and it seems that there is not a great deal of change throughout the year, in contrast with conditions described by Blegvad (1925) for enclosed shallow waters.

On the basis of both numbers and frequency of occurrence the more important elements of the fauna include the following species:—

Dominants or characteristic species:
Nephthys incisa, Abra prismatica, Corbula gibba.

Influents or abundant species:
Glycera rouxi, Goniada maculata, Lumbriconereis spp., *Owenia fusiformis, Pectinaria* spp., *Trichobranchus glacialis, Phoronis mulleri, Iphinoe serrata, Diastylis lucifera, Westwoodilla caecula, Schistomysis ornata, Crangon allmanni, Nephrops norvegicus, Anapagurus laevis, Nucula sulcata, Cardium scabrum, Cultellus pellucidus, Turritella communis, Amphiura* spp., *Echinocardium flavescens, Echinocyamus pusillus.*

Common species:
Astrorhiza limicola, Thecocarpus myriophyllum, Amphiporus sp., *Aphrodite aculeata, Notocirrus scoticus, Onuphis conchylega, Laonice cirrata, Prionospio* spp., *Chaetozone setosa, Diplocirrus glaucus, Notomastus latericeus, Myriochele heeri, Amphicteis gunneri, Terebellides stroemi, Phascolosoma procerum, Phascolion strombi, Scalpellum scalpellum, Peltogaster paguri, Eudorella emarginata, Diastyloides biplicata, Hippomedon denticulatus, Ampelisca* spp., *Harpinia pectinata, Epimeria cornigera, Eusirus longipes, Cheirocratus intermedius, Lembos longipes, Erythrops serrata, Pandalus montagui, Pandalina brevirostris, Alphaeus ruber, Pontophilus echinulatus, Dosinia lupinus, Chlamys opercularis, Mysia undata, Cardium ovale, Solecurtus chamasolen, Calopodium pinna, Dentalium entalis, Aporrhais pes-pelicani, Mangelia brachystoma, Ophiura albida, O. affinis, Leptosynapta inhaerens.*

There are no considerable changes from the fauna described for the muddy sand ground to the south-west of the Isle of Man during the period from 1947 to 1950 (Jones 1951). The mean wet weight of animals on the fine muddy sand at that time was 47.3 g/m², but since this estimate was made from fewer samples covering a larger area it would not be safe to conclude that there is any significance in the lower figure compared with that obtained in 1952.

COMPARATIVE SAMPLES

To provide comparative data two series of ten 0·1 m² hauls were taken with the bottom sampler during June 1953 in the muddy sand area off Bradda Head and one of twenty 0·1m² samples off the Cumberland coast in the area worked in 1948-1950 (Jones 1952). The samples off the Isle of Man were taken at two stations, one about ½ mile to seaward of the other, in 37-39 and 34-37 fm respectively. The deposit at the deeper station, F2, was finer than that at the shallower, F1, as shown by analysis (Table 1). Comparison of the animals in F1 and F2 (Table 5) shows that even a small alteration in position with a slight difference in deposit may be accompanied by a considerable change in the fauna and difference in biomass. The fauna of F1 is comparable to that in A, D and E of the main series in 1952, while that of F2 is comparable to C. The rough weight of F2 was 41·9 g/m², close to that for C of 43·6 g/m² in the same month a year previously. The wet weight of F1, however, was 213·6 g/m², a good deal higher than the figure of 75·3 g/m² found for A, D and E. A large part but not the whole of this difference was due to the greater numbers of *Corbula gibba* found per unit area in F1—526/m² compared with a mean of 260/m² in A, D and E. The remaining weight difference was mainly due to the presence of a number of large specimens of *Dosinia lupinus* and *Brissopsis lyrifera* in F1, together with a quantity of *Molgula occulta*, while these were fewer or absent in A, D and E. The numbers of *Corbula* may be significant of an increased population of the species during 1953. Analysis of variance from the data in Table 3 shows that while the differences in numbers of *Corbula* in Series A, D and E are not significant ($F = 0{\cdot}18$, 5% point $= 3{\cdot}35$) those between A and F1 are highly significant ($F = 10{\cdot}47$, 1% point $= 8{\cdot}28$). It would appear from this result that there may be changes in the biomass in the area

Table 4. *Numbers of species in runner-dredge hauls on muddy sand ground off Port Erin, 1952-1953*

	Serial Number					
	B1	B2	C1	D1	D2	E1
	15 Apr. 1952	15 Apr. 1952	4 June 1952	17 Nov. 1952	17 Nov. 1952	9 Jan. 1953
Depth (fn):	34-37	33	37	32-37	36-38	35-37
FORAMINIFERA						
Astrorhiza limicola Sandahl	—	—	—	4	1	220
COELENTERATA						
Halecium beani (Johnston)	—	1	—	—	—	—
Sertularella polyzonias (L.)	—	—	—	—	1	—
Abietinaria abietina (L.)	1	3	—	—	—	—
Diphasia pinaster (Ellis & Solander)	—	3	—	—	—	—
Nemertesia ramosa (Lamouroux)	—	3	—	—	—	—
Thecocarpus myriophyllum (L.)	3	6	—	—	—	4
NEMERTINEA						
Amphiporus sp.	—	—	—	—	—	1
CHAETOGNATHA						
Sagitta elegans Verrill	—	—	100	—	—	—
POLYCHAETA						
Aphrodite aculeata L.	1	2	19	4	5	1
Lepidonotus squamatus (L.)	—	—	—	1	—	—
Harmothoe spp.	—	1	—	2	1	2
Lagisca extenuata (Grube)	2	4	—	—	—	—
Phyllodoce sp.	—	—	6	—	—	—
Eulalia sanguinea Oersted	—	—	—	—	1	—
Notophyllum foliosum (Sars)	1	—	—	—	—	—
Ophiodromus flexuosus Delle Chiaje	—	—	1	-	—	—
Nereis zonata Malmgren	1	4	—	-	—	—
N. fucata Savigny	—	—	—	2	—	3
Nephthys incisa Malmgren	—	—	14	8	6	4
Glycera rouxi Aud. & M.-Edw.	—	—	—	-	1	—
Goniada maculata Oersted	—	—	—	-	3	—
Eone nordmanni Malmgren	—	—	—	1	—	—
Onuphis conchylega Sars	1	32	—	—	2	2
Lumbriconereis impatiens Claparède	—	—	—	—	3	-
Sphaerodorum claparedii Greeff	—	—	—	—	1	—
Diplocirrus glaucus Haase	—	—	1	—	18	2
Ammotrypane aulogaster Rathke	—	—	1	—	1	-
A. cylindricaudatus Hansen	—	—	—	—	1	—
Notomastus latericeus Sars	—	—	1	—	—	—
Pectinaria auricoma (O. F. Müller)	—	—	1	1	4	1
Ampharete grubei Malmgren	—	—	—	—	2	—
Amphicteis gunneri (Sars)	—	—	1	—	—	—
Thelepus cincinnatus (Fabricius)	—	—	—	3	1	—
Terebellides stroemi Sars	1	—	—	—	—	—
Hydroides norvegica Gunnerus	—	—	—	—	—	1
Spirorbis spirillum (L.)	—	100	—	—	—	—
HIRUDINEA						
Pontobdella muricata (L.)	—	—	—	—	1	—
GEPHYREA						
Phascolosoma procerum Möbius	—	—	3	6	—	2
Phascolion strombi (Montagu)	4	9	2	2	3	1
CRUSTACEA						
Anomalocara patersoni Templeton	3	1	—	—	—	—
Balanus porcatus da Costa	—	—	—	—	15	—

	Serial Number					
	B1	B2	C1	D1	D2	E1
Scalpellum scalpellum (L.)	1	2	5	—	1	—
Peltogaster paguri Rathke	1	—	4	2	—	13
Nebalia bipes (Fabricius)	—	—	4	—	—	—
Iphinoe serrata Norman	1	—	6	70	450	120
Eudorella emarginata (Kröyer)	—	—	7	—	1	2
Campylaspis rubicunda (Lilljeborg)	—	—	—	1	4	1
C. glabra G. O. Sars	—	—	—	—	1	—
Diastylis lucifera (Kröyer)	3	—	170	15	50	17
D. laevis Norman	—	—	15	—	—	7
Diastyloides biplicata G. O. Sars	—	—	17	12	40	12
Gnathia sp.	—	—	1	—	—	—
Astacilla longicornis Sowerby	1	4	2	—	—	—
Arcturella dilatata G. O. Sars	—	—	—	—	—	1
Hippomedon denticulatus (Bate)	1	—	2	7	13	14
Tryphosites longipes (Bate & Westwood)	—	—	—	8	1	1
Scopelocheirus crenatus Bate	—	2	—	—	—	2
Perrierella audouiniana (Bate)	—	—	4	—	—	—
Stegocephaloides christianensis (Boeck)	—	—	—	—	1	—
Ampelisca spinipes Boeck	1	4	—	8	15	3
A. tenuicornis Lilljeborg	1		70	5	10	6
A. typica (Bate)	—	—	—	—	2	—
A. macrocephala Lilljeborg	—	—	—	—	2	—
Harpinia pectinata Sars	—	—	15	5	75	42
Leucothoe lilljeborgi Boeck	—	—	—	—	3	1
Stenothoe marina (Bate)	—	—	4	1	—	—
Metopa borealis Sars	—	—	—	1	—	1
Panoploea minuta (Sars)	—	-	—	—	4	2
Westwoodilla caecula (Bate)	12	1	45	3	8	102
Apherusa bispinosa (Bate)	—	1	5	—	—	4
Epimeria cornigera (Fabricius)	1	12	11	—	1	3
Nototropis vedlomensis (Bate & Westwood)	—		10	—	2	1
Eusirus longipes Boeck	1	-	9	15	25	11
Cheirocratus intermedius Sars	4	—	8	1	2	—
Melita obtusata Montagu	—	—	1	—	—	—
Maera othonis (M.-Edw.)	—	—	5	—	—	—
Lembos longipes (Lilljeborg)	2	—	20	1	2	—
Photis longicaudata (Bate & Westwood)	—	1	—	—	—	—
Eurystheus erythrophthalmus (Lilljeborg)	1	1	2	—	—	—
Podoceropsis nitida Stimpson	—	—	—	—	—	5
Ericthonius brasiliensis (Dana)	—	—	2	—	—	—
Phtisica marina Slabber	—	5	3	—	—	1
Meganycliphanes norvegica (M. Sars)	—	—	—	—	—	3
Nyctiphanes couchi (Bell)	—	—	—	—	1	—
Siriella jaltensis Czerniavsky	—	—	—	—	—	2
Erythrops serrata (G. O. Sars)	—	—	10	9	—	15
Mysidopsis angusta (G. O. Sars)		—	—	1	—	—
M. didelphys (Norman)	—	—	1	—	—	—
Schistomysis ornata G. O. Sars	200	100	500	—	—	—
Pseudomma affine G. O. Sars	—	—	—	5	—	—
Processa canaliculata Leach	—	—	—	—	9	—
Pandalus montagui Leach	1	1	—	—	8	6
P. bonnieri Caullery	—	—	-	15	20	—
Pandalina brevirostris (Rathke)	6	57	2	4	7	40
Alphaeus ruber M.-Edw.	—	—	1	1	15	2
Crangon allmanni Kinahan	24	8	52	55	110	86
Pontophilus bispinosus (Hailstone & Westwood)	—	—	—	—	15	35
P. echinulatus (M. Sars)	2	5	—	20	65	24
P. spinosus (Leach)	2	2	2	2	6	—
Nephrops norvegicus L.	10	—	11	15	42	15
Galathea intermedia Lilljeborg	—	—	—	—	—	2
G. dispersa Bate	—	11	—	—	—	—

	Serial Number					
	B1	B2	C1	D1	D2	E1
Munida bamffia (Pennant)	—	—	—	2	—	—
Porcellana longicornis L.	—	1	—	—	—	—
Callianassa tyrrhena (Petagna)	—	1	—	—	—	—
Eupagurus bernhardus (L.)	—	—	—	1	—	2
E. prideauxi (Leach)	—	—	—	5	2	31
Anapagurus laevis (Thompson)	81	37	251	80	86	430
Portunus holsatus Fabricius	—	—	—	11	14	2
Cancer pagurus L.	—	—	—	—	1	—
Goneplax angulata Pennant	—	—	—	1	2	—
Pinnotheres pisum (Pennant)	—	—	1	—	—	—
Ebalia tuberosa (Pennant)	—	3	—	—	—	—
E. tumefacta (Montagu)	—	—	—	1	—	—
Eurynome aspera (Pennant)	—	3	—	—	—	—
Hyas coarctatus Leach	3	11	—	—	—	2
Inachus dorsettensis (Pennant)	—	8	—	—	—	—
Macropodia rostrata (L.)	—	—	3	—	—	—
M. longirostris (Fabricius)	—	10	—	6	6	7
PYCNOGONIDA						
Anoplodactylus petiolatus (Kröyer)	—	—	—	1	1	—
MOLLUSCA						
Proneomenia aglaopheniae Kovalevsky & Marion	—	—	—	—	—	1
Chaetoderma nitidulum Lovèn	—	—	—	—	6	—
Nucula sulcata Bronn	15	1	28	10	12	15
Pecten maximus (L.)	—	1	—	—	—	—
Chlamys opercularis (L.)	10	36	2	2	4	—
Lima subauriculata (Montagu)	—	6	1	1	7	2
Astarte sulcata (da Costa)	1	1	—	—	—	—
Thyasira flexuosa (Montagu)	—	—	—	—	1	—
Myrtea spinifera (Montagu)	—	—	—	1	4	—
Kellia suborbicularis (Montagu)	1	—	—	—	—	—
Abra prismatica (Montagu)	12	2	283	60	600	58
Spisula elliptica (Brown)	—	—	—	6	3	6
Mysia undata (Pennant)	2	1	39	3	—	—
Dosinia lupinus (Montagu)	1	—	—	1	—	1
Venus striatula (da Costa)	—	—	—	1	1	1
V. fasciata (da Costa)	—	—	1	—	—	—
Cardium ovale Sowerby	5	1	2	2	—	3
C. scabrum Philippi	265	470	1	18	55	126
Corbula gibba (Olivi)	355	63	57	64	15	54
Cultellus pellucidus (Pennant)	2	—	10	8	6	7
Hiatella arctica (L.)	—	—	3	—	-	—
Calopodium pinna (Montagu)	1	2	—	5	1	7
Dentalium entalis L.	1	—	—	1	1	4
Calliostoma zizyphinum (Lamarck)	—	64	—	—	—	—
C. papillosum (da Costa)	1	6	1	—	—	1
Natica poliana Forbes	1	1	—	—	—	1
Odostomia eulimoides Hanley	—	1	—	—	—	—
Balcis alba (da Costa)	—	7	—	—	—	—
Turritella communis Risso	122	24	200	94	29	83
Aporrhais pes-pelicani da Costa	15	16	—	—	—	2
Neptunea antiqua (L.)	—	1	—	—	—	—
Trophon muricatus (Montagu)	2	25	—	1	—	—
Mangelia coarctata (Forbes)	14	12	—	—	—	—
M. brachystoma Philippi	5	—	6	24	4	48
Philbertia linearis (Montagu)	—	1	—	—	—	—
Tricla lignaria Leach	—	1	9	—	—	—
Hermania catena (Montagu)	—	—	—	—	1	—
Pleurobranchus membranaceus (Montagu)	—	2	—	—	—	1
Onchidoris pusilla (Alder & Hancock)	1	—	—	—	—	—
O. oblonga (Alder & Hancock)	—	6	—	—	—	—
Eubranchus tricolor Forbes	—	—	—	—	—	2

	Serial Number					
	B1	B2	C1	D1	D2	E1
Idulia coronata (Gmelin)	—	1	—	—	—	—
Rossia macrosoma (Oken)	—	—	8	—	—	2
BRYOZOA						
Cellaria fistulosa (L.)	—	5	—	—	—	—
ECHINODERMATA						
Antedon bifida (Pennant)	—	3	—	—	—	—
Asterias rubens L.	—	—	—	1	—	2
Porania pulvillus (Müller)	—	—	—	—	—	2
Ophiothrix fragilis (Abildgaard)	—	8	—	—	—	1
Amphiura chiajei Forbes	—	—	3	—	2	—
Ophiura texturata Lamarck	3	14	—	—	—	1
O. albida Forbes	30	690	—	—	—	—
O. affinis Lütken	24	130	—	—	2	—
Echinus esculentus L.	—	4	2	—	—	—
Psammechinus miliaris (Gmelin)	—	1	—	—	—	—
Echinocardium flavescens (Müller)	—	—	—	1	—	6
Echinocyamus pusillus (Müller)	7	2	—	1000	45	64
PISCES						
Nerophis lumbriciformis (Pennant)	—	—	—	—	1	—
Onos cimbrius (L.)	—	—	—	1	1	2
Centronotus gunnellus (L.)	—	—	—	—	—	1
Callionymus lyra L.	1	—	—	1	3	2
Gobius elongatus Canestrini	—	1	—	5	9	1
Gadus esmarkii Nilsson	—	—	—	3	—	—

Table 5. *Numbers per m², occurrence and wet weights of all species on the muddy sand grounds off Port Erin and the Cumberland coast, June 1953*

Series :	F1			F2			S		
No. of samples (each 0·1 m²)	10			10			20		
Date (1953):	29 June			29 June			25 June		
Depth (fm):	34-37			37-39			11		
	No.	Occ.	Wt.	No.	Occ.	Wt.	No.	Occ.	Wt.
FORAMINIFERA									
Astrorhiza limicola Sandahl	113	10	.	—	—	—	—	—	—
COELNENTERATA									
Cerianthus lloydi Gosse	1	1	.	—	—	—	1	1	.
NEMERTINEA									
Amphiporus sp.	7	7	.	4	3	.	24	10	.
POLYCHAETA									
Aphrodite aculeata L.	1	1	.	—	—	—	4	4	.
Harmothoe spp.	5	3	.	2	2	.	—	—	—
Lagisca extenuata (Grube)	1	1	.	—	—	—	—	—	—
Pholoe minuta Fabricius	1	1	.	—	—	—	9	7	.
Polynoe kinbergi (Malmgren)	—	—	—	—	—	—	1	1	.
Sthenelais limicola (Ehlers)	—	—	—	—	—	—	6	4	.
Eulalia sp.	1	1	.	—	—	—	—	—	—
Podarke pallida Claparède	—	—	—	—	—	—	1	1	.
Ophiodromus flexuosus Delle Chiaje	1	1	.	—	—	—	—	—	
Nereis longissima Johnston	—	—	—	—	—	—	1	1	.
Nephthys hombergi Lamarck	—	—	—	—	—		39	10	.
N. incisa Malmgren	9	6	.	15	10	.	3	3	.
Glycera rouxi Aud. & M.-Edw.	8	6	.	5	5	.	2	2	.
Goniada maculata Oersted	4	4	.	2	2	.	1	1	.

Series:	F1			F2			S		
	No.	Occ.	Wt.	No.	Occ.	Wt.	No.	Occ.	Wt.
Eone nordmanni Malmgren	1	1	.	1	1	.	2	2	.
Lumbriconereis hibernica McIntosh	6	6	.	14	9	.	8	7	.
L. gracilis Ehlers	—	—	—	2	1	.	65	10	.
Nolocirrus scoticus McIntosh	2	2	.	—	—	—	—	—	—
Eunicid sp.	—	—	—	—	—	—	1	1	.
Aricia cuvieri Aud. & M.-Edw.	1	1	.	—	—	—	—	—	—
Laonice cirrata (Sars)	3	2	.	—	—	—	—	—	—
Nerinides tridentata Southern	1	1	.	—	—	—	—	—	—
Spio filicornis (Müller)	1	1	.	7	4	.	—	—	—
Polydora flava Claparède	3	2	.	—	—	—	—	—	—
Prionospio steenstrupi Malmgren	7	4	.	1	1	.	—	—	—
Magelona papillicornis (F. Müller)	—	—	—	—	—	—	4	3	.
Chaetozone setosa Malmgren	4	3	.	5	3	.	—	—	—
Heterocirrus sp.	—	—	—	—	—	—	1	1	.
Diplocirrus glaucus Haase	7	5	.	10	7	.	1	1	.
Scalibregma inflatum Rathke	—	—	—	3	3	.	—	—	—
Ammotrypane aulogaster Rathke	—	—	—	—	—	—	1	1	.
A. cylindricaudatus Hansen	1	1	.	—	—	—	—	—	—
Maldanid sp.	—	—	—	—	—	—	1	1	.
Clymene affinis (Sars)	—	—	—	—	—	—	2	2	.
Notomastus latericeus Sars	—	—	—	5	4	.	—	—	—
Owenia fusiformis Delle Chiaje	155	10	.	12	6	.	10	6	.
Myriochele heeri Malmgren	70	10	.	13	7	.	—	—	—
Pectinaria auricoma (Müller)	10	8	.	1	1	.	6	5	.
P. belgica (Pallas)	—	—	—	—	—	—	1	1	.
P. koreni Malmgren	15	8	.	—	—	—	5	4	.
Ampharete grubei Malmgren	11	7	.	3	3	.	2	2	.
Amphicteis gunneri (Sars)	2	2	.	1	1	.	2	1	.
Sabellides octocirrata Sars	3	3	.	—	—	—	—	—	—
Lanice conchilega Pallas	1	1	.	—	—	—	—	—	—
Polycirrus sp.	2	2	.	—	—	—	—	—	—
Streblosoma bairdi (Malmgren)	—	—	—	—	—	—	55	10	.
Trichobranchus glacialis Malmgren	8	5	.	2	2	.	9	7	.
Terebellides stroemi Sars	1	1	.	1	1	.	1	1	.
Sabellid sp.	3	2	.	—	—	—	—	—	—
Hydroides norvegica Gunnerus	1	1	.	—	—	—	—	—	—
GEPHYREA									
Phascolosoma procerum Möbius	1	1	.	—	—	—	10	8	.
Phascolion strombi (Montagu)	1	1	.	—	—	—	1	1	.
PHORONIDEA									
Phoronis mulleri de Selys Longchamps	24	10	.	12	5	.	130	10	.
Total above			4·29			4·93			8·44
CRUSTACEA									
Nebalia bipes (Fabricius)	—	—	.	2	1	.	—	—	—
Iphinoe serrata Norman	18	8	.	1	1	.	—	—	—
Eudorella emarginata (Krøyer)	—	—	—	1	1	.	—	—	—

Series:	F1			F2			S		
	No.	Occ.	Wt.	No.	Occ.	Wt.	No.	Occ.	Wt.
Diastylis rathkei (Kröyer)	—	—	—	—	—	—	12	8	.
D. laevis Norman	2	2	.	3	2	.	—	—	—
D. lucifera (Kröyer)	14	7	.	—	—	—	—	—	—
Cirolana borealis Lilljeborg	2	2	.	1	1	.	—	—	—
Eurydice inermis Hansen	1	1	.	—	—	—	—	—	—
Hippomedon denticulatus (Bate)	1	1	.	—	—	—	—	—	—
Tryphosites longipes (Bate & Westwood)	1	1	.	—	—	—	—	—	—
Ampelisca spp.	95	10	.	42	10	.	98	7	.
Harpinia antennaria Meinert	—	—	—	—	—	—	1	1	.
H. pectinata Sars	5	3	.	1	1	.	—	—	—
H. crenulata Boeck	—	—	—	3	1	.	—	—	—
Leucothoe lilljeborgi Boeck	—	—	—	1	1	.	—	—	—
Metopa borealis Sars	1	1	.	—	—	—	—	—	—
Westwoodilla caecula (Bate)	7	4	.	—	—	—	—	—	—
Nototropis vedlomensis (Bate & Westwood)	2	2	.	—	—	—	—	—	—
Eusirus longipes Boeck	1	1	.	1	1	.	—	—	—
Cheirocratus intermedius Sars	1	1	.	2	1	.	—	—	—
Maera othonis (M.-Edw.)	2	2	.	—	—	—	—	—	—
Lembos longipes (Lilljeborg)	2	1	.	—	—	—	—	—	—
Photis longicaudata (Bate & Westwood)	2	2	.	—	—	—	—	—	—
Corophium affine Bruzelius	4	3	.	—	—	—	—	—	—
Alphaeus ruber M.-Edw.	1	1	0·28	1	1	0·08	—	—	—
Corystes cassivelaunus (Pennant)	—	—	—	—	—	—	1	1	.
Brachyuran megalopa	1	1	.	1	1	.	—	—	—
Total Crustacea and other groups where not included separately			2·43			1·11			1·01
MOLLUSCA									
Chaetoderma nitidulum Lovèn	1	1	.	—	—	—	—	—	—
Nucula turgida Leckenby & Marshall	—	—	—	—	—	—	3	3	.
N. sulcata Bronn	6	4	1·26	21	8	4·89	—	—	—
Thyasira flexuosa (Montagu)	—	—	—	3	2	.	8	4	.
Myrtea spinifera (Montagu)	—	—	—	1	1	.	—	—	—
Montacuta ferruginosa (Montagu)	2	2	.	2	1	.	9	5	.
Mysella bidentata (Montagu)	—	—	—	—	—	—	190	10	0·47
Cardium echinatum L.	—	—	—	—	—	—	2	2	0·30
C. scabrum Philippi	13	7	0·38	—	—	—	—	—	—
Dosinia lupinus (Montagu)	9	5	18·17	—	—	—	2	1	—
Venus striatula (da Costa)	2	2	1·07	—	—	—	17	8	1·97
Gari fervensis (Gmelin)	—	—	—	—	—	—	3	3	0·42
Abra alba (Wood)	—	—	—	—	—	—	14	7	.
A. prismatica (Montagu)	73	10	0·83	271	10	4·10	—	—	—
Solecurtus chamasolen (da Costa)	2	2	4·19	2	2	3·87	—	—	—
Cultellus pellucidus (Pennant)	9	5	0·25	1	1	0·32	5	3	0·12
Spisula subtruncata (da Costa)	—	—	—	—	—	—	1	1	0·15
Corbula gibba (Olivi)	526	10	143·98	18	7	.	8	5	0·23
Thracia phaseolina (Lamarck)	—	—	—	2	2	.	1	1	.
T. pubescens (Montagu)	—	—	—	1	1	0·38	—	—	—
Lyonsia norvegica (Gmelin)	1	1	0·14	—	—	—	—	—	—
Cuspidaria costellata (Deshayes)	1	1	.	—	—	—	—	—	—
Dentalium entalis L.	8	5	0·10	—	—	—	—	—	—

Series:	F1			F2			S		
	No.	Occ.	Wt.	No.	Occ.	Wt.	No.	Occ.	Wt.
Turritella communis Risso	16	6	8·31	22	8	8·16	1	1	.
Natica poliana Forbes	1	1	0·10	—	—	—	—	—	—
Eulima trifasciata (Adams)	1	1	.	—	—	—	—	—	—
Mangelia brachystoma Philippi	—	—	—	1	1	.	—	—	—
Cylichna cylindracea (Pennant)	—	—	—	—	—	—	14	7	.
Philine aperta Ascanius	—	—	—	—	—	—	6	4	0·36
ECHINODERMATA									
Asterias rubens L.	—	—	—	—	—	—	1	1	.
Ophiura sp.	—	—	.	—	—	—	2	2	.
Amphiura chiajei Forbes	4	4	0·14	4	2	0·61	—	—	—
A. filiformis (Müller)	21	8	1·09	2	2	0·30	993	10	146·09
Echinocardium cordatum (Pennant)	—	—	—	—	—	—	19	8	23·72
E. flavescens (Müller)	17	4	2·09	—	—	—	—	—	—
Brissopsis lyrifera (Forbes)	21	6	17·25	5	5	13·65	—	—	—
Echinocyamus pusillus (Müller)	4	3	0·07	—	—	—	—	—	—
Leptosynapta inhaerens (Müller)	2	1	0·25	—	—	—	2	1	.
Labidoplax buski (McIntosh)	13	6	0·22	—	—	—	—	—	—
TUNICATA									
Ascidiella scabra (Müller)	3	1	0·84	—	—	—	—	—	—
Molgula occulta Kupffer	68	8	6·91		—	—	—	—	—
Total individuals	1487			535			1733		
Total species	85			50			59		
Total wet weight (g)			213·65			41·87			203·00

investigated over a period of time caused by the success or otherwise of the spatfall of *Corbula*, as has frequently been noted for other areas in the case of other lamellibranch species (Holme 1953, p. 44), and for *Corbula* itself in Danish waters. Thorson (1946) shows that species such as *Corbula* whose larvae have a long pelagic life vary in biomass from year to year much more than those with a short pelagic phase.

Comparing F1 with F2, the considerably smaller biomass of F2 is largely the reflection of an impoverished fauna on the more muddy ground. Analysis of variance for wet weights of samples shows the difference to be highly significant ($F = 27{\cdot}08$, 1% point $= 8{\cdot}28$); 85 species were present in F1 and only 50 in F2. Specifically the more important differences were that: *Astrorhiza limicola* was present in all ten samples of F1 but completely absent from F2; *Owenia fusiformis*, *Myriochele heeri* and *Pectinaria* spp. were much more abundant in F1; *Iphinoe serrata* and *Diastylis lucifera* occurred in most samples in F1 but only in one of F2; *Cardium scabrum*, *Dosinia lupinus*, *Cultellus pellucidus*, *Corbula gibba* and *Dentalium entalis* were much more abundant in F1; *Amphiura filiformis*, *Echinocardium flavescens* and *Labidoplax buski* were fairly well represented in F1 and either few or absent in F2; *Molgula occulta* was present in most samples in F1 and absent in F2. Only *Abra prismatica*, while present in all samples in both series, was considerably more abundant in F2 than in F1, while *Nucula sulcata* was somewhat more important. Most of the difference in biomass, however, was due to the presence of

526 specimens of the single species *Corbula gibba* with a rough weight of 114 g in F1, compared with only 18 small specimens of negligible weight in F2.

The bottom deposit from which the S series was taken off the Cumberland coast contains rather more of the finer grades of deposit than the F2 samples off Beadnell Head. The biomass of the series, however, was only slightly lower than that of the F1 series (Table 1), and much higher than that of F2. Nevertheless from the similarity of the deposit, S should be compared with F2. The number of species present is only slightly higher than that of F2 (59 against 56), but the number of specimens was much greater (1783 against 585). A very large part of this last difference—and of the difference in wet weight was due to the presence of 668 specimens of *Amphiura filiformis* in S, weighing 146 g, compared with two specimens in F2, weighing 0·3 g. That the fauna of S is more comparable with F2 than with F1 is shown by the absence of *Astarte borealis*, *Cardium exiguum*, *Echinocardium flavescens*, *Lutraria elliptica* and *Mysella bidentata* from S and F2, and the much smaller numbers of *Corbula gibba* compared with F1. However, S shows a number of differences from F2 other than the numbers of *Amphiura*, possibly correlated with the difference in depth of the two series. A number of polychaetes are present only in S and rather fewer only in F2, while the place of *Nephtys cæca* in F2 is taken by *N. hombergi* in S. *Diastylis rathkei* takes the place in S of *D. laevis* in F2. *Nucula nucula* takes the place of *N. sulcata*. Also also the place of *Abra prismatica* and *Echinocardium cordatum* the place of *Echinocyamus pusillus*. In S *Phoronis muelleri* is more important and *Mysella bidentata* is common, while it is absent in F2, as were *Phascolosoma procerum*, *Venus striatula*, *Cylichna cylindracea* and *Philine aperta*. On the other hand *Turritella communis* was more important in F2 than in S. Most of the species mentioned above in S seem to be more characteristic of very shallow depths than those in F2 (cf. Friel 1928), though why this should be so is unknown.

The position of the S series was fixed by means of fairly close landmarks and may be stated with some confidence. It is therefore possible to compare it with the samples taken in the same area by the same methods three years previously on 28 May 1950 (Jones 1952). The S series was not taken in exactly the position of any of the 1950 stations, but it lay in a position nearest to Station 49 of 1950, and might therefore be expected to show a similarity to the fauna of this station.

If the S series is split into two lots of ten samples each in order of taking (S1 and S2), analysis of variance shows that the wet weights are not significantly different ($F = 1{\cdot}89$, 5%, point $= 4{\cdot}41$). The rough weights of S1 and S2 (1856 and 2203 g m^{-2}) are somewhat lower than that of 49 (3275 g m^{-2}). It is not possible to test total weights of the S series and the 1950 series by analysis since sample weights were not measured separately in the latter, but the numbers of the most abundant species present on both occasions, *Amphiura filiformis*, may be used. Here again analysis of variance between S1 and S2 shows that there is no significant difference between numbers (totals 981 and 1004, $F = 0{\cdot}08$, 5%, point $= 4{\cdot}41$). Between S1 and 49 (total 1106) and S2 and 49 there is again no significant difference—S1 and 49, $F = 1{\cdot}59$, 5%, point $= 4{\cdot}41$; S2 and 49, $F = 1{\cdot}49$, 5%, point $= 4{\cdot}41$.

The number of individuals in the S series was higher than in Stn. 49 –1733 and 1412 respectively for all animals counted, adult and immature. Rather more species of polychaetes were identified during 1953, as were 130 specimens of *Phoronis mulleri*, not distinguished in 1950 though probably present. There seem to be no differences between numbers for the species identified during the two years sufficiently large to be significant, with the possible exception of those in the case of *Cultellus pellucidus*. Here 125 were obtained in 1950 and only 3 in 1953. However, the larger number present at Stn. 49 appeared to be anomalous compared with the catch at other stations on the muddy sand in 1950, and was probably due

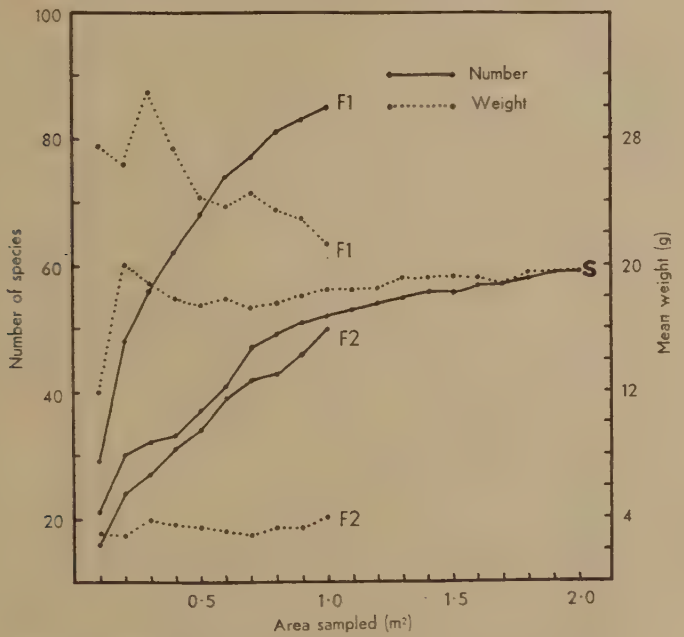


Fig. 2. Cumulative curves showing the numbers of species and mean wet weights of animals in successive samples for Stns. F1, F2 and S.

to a local aggregation, so that the two years cannot be safely compared. It therefore seems probable that there has been little change in the composition of the fauna off the Cumberland coast during the period of three years between May 1950 and June 1953.

The comparisons made above have been based mainly on numbers of specimens and wet weights, but for investigations into the possible causes of differences in biomass it is necessary to use a criterion less liable to error. Errors may arise during the taking of the samples or their subsequent treatment. Holme (1953) shows the relation between numbers of species obtained and area sampled. Cumulative curves demonstrate that for 0.05 m² samples a total area of less than 0·5 m² per station is inadequate for qualitative sampling. Cumulative curves for

the three stations F1, F2 and S, are shown in Fig. 2. They show that for a faunal survey on these grounds 1 m² is the minimum adequate area, and that 2 m² would be more satisfactory. In the case of F1, 1 m² is clearly inadequate as the curve is still rising steeply at this point. For biomass estimations again 1 m² is the minimum area for F2 and S, while for F1 it is evident that little reliance can be placed on the results from the area of 1·0 m² sampled. Holme's sampler, however, would probably give reliable results from a smaller total area as each sample covers only half the area of the 0·1 m² van Veen grab. It would appear that the fauna on the F1 ground is irregularly distributed and as the deposit is somewhat harder than that on F2 the grab may be less reliable.

Ursin (1954) compares the 0·2 m² van Veen and Petersen grabs, showing that the van Veen sampler is superior on fine sand, and that skill in using the gear affects results. Ursin also shows that the number of specimens brought up increases steadily with the amount of deposit in the sample up to about 10-16 litres for the 0·2 m² grab. For larger samples the number of specimens remains fairly constant. The van Veen grab seems to be of the same order of efficiency as Holme's sampler, and is probably reliable on muddy sand, while the area of 1·0 m² for each station should avoid any major errors, except in the case of Stn. F1, in estimation either of the composition of the fauna or of the biomass. The mean volume of bottom material brought up by the 0·1 m² van Veen grab in this investigation was 5·8 l. at Stn. F2. This compares favourably with the means of 7·8 and 11·1 l. obtained by Ursin on muddy sand in 1951 and 1952 respectively, using the much heavier 0·2 m² grab, and with Holme's results of about 3 l. for each sample with his 0·05 m² single-scoop sampler.

Holme (1953) estimates losses through the meshes of a 2·2 mm sieve at about 10% of the total dry weight, while Mare (1942) found that on muddy sand about 30% of the wet weight passed through this size of sieve. Off the Isle of Man and the Cumberland coast the weight lost in this way was not more than 10%.

Although there is a strong correlation between numbers and weight for abundant species taken in a single series of hauls (in the case of *Corbula gibba* in F1 $r = 0{\cdot}996$, 1% point $= 0{\cdot}765$) the weight per individual must obviously increase with growth, so that conclusions concerning biomass cannot safely be drawn from data concerning numbers present. Since it is not possible to ensure that the ratio of water to tissue is always the same in different samples when wet weight is measured, and because calcareous matter is unlikely to be limited by any substance in sea water other than calcium, of which large amounts are always present, the dry weight less calcareous material has been determined. The procedure adopted was similar to that described by Holme (1953) with the following differences: the animals were preserved in 5% formalin and not in alcohol, and it is presumed that there was no appreciable loss in weight through solution in this medium; Mollusca were not removed from their shells by hand, but the shells were dissolved in dilute hydrochloric acid together with other calcareous matter; the gut contents of *Echinocardium* and *Brissopsis* were removed by careful washing.

Details of wet and dry weights are shown in Table 6. The mean ratio of dry

weight to wet weight for the three stations is for F1—6·2, F2—6·5, S1—9·9%. The difference is presumably due to the greater quantity of *Amphiura*, which has a smaller proportion of calcium in the skeleton, in S1 compared with F1 and F2 in which lamellibranchs with much calcium in the shell were more important.

Table 6. *Sample weights (g/m²), June 1953*

	Series								
	F1			F2			S1		
Number of Sample	Wet	Dry	Dry/Wet (%)	Wet	Dry	Dry/Wet (%)	Wet	Dry	Dry/Wet (%)
1	27·58	1·97	7·1	3·03	0·13	4·3	12·02	1·31	10·9
2	25·90	1·48	5·7	2·63	0·35	13·3	28·00	2·71	9·7
3	39·22	2·65	6·7	5·99	0·25	4·1	16·41	1·55	9·4
4	17·24	0·87	5·1	2·63	0·17	6·5	14·92	1·58	10·3
5	11·15	0·77	6·9	3·34	0·23	6·9	16·13	1·60	9·9
6	19·78	1·36	7·4	1·33	0·17	12·8	19·99	1·98	9·9
7	32·06	1·67	5·2	1·39	0·08	5·8	14·42	1·46	10·1
8	14·49	0·79	5·4	7·33	0·37	5·0	19·40	1·84	9·5
9	19·86	1·24	6·3	2·85	0·21	7·4	21·98	2·24	10·2
10	6·37	0·40	6·3	11·35	0·75	6·6	22·36	2·15	9·6
Totals	213·65	13·20		41·87	2·71		185·63	18·42	
Means			6·2			6·5			9·9

Holme's figure of about 20% for Plymouth grounds was based on fresh weights less calcium carbonate, and if the ratios for F1, F2 and S1 are calculated on this basis they are 19.4 ,17·3 and 17·9% respectively, which are fairly consistent and not very different from the results obtained by Holme. It will be noted that whereas the wet weight of F1 (213·7 g m²) was greater than that of S1 (185·6 g m²) the dry weight after acid treatment was smaller, 13·2 compared with 18·4 g m². This inversion was certainly the result of the large number of *Corbula* in F1, of which a large proportion by weight was shell which was dissolved out by the acid. It is evident that the rough weight with calcareous matter is an unreliable guide to the amount of organic matter present.

At each station the ratio of dry weights to wet weights is fairly constant throughout the samples, except for two rather high values in F2, and from this it appears that wet weights might be sufficiently reliable for biomass comparisons on the same ground over a period of time, provided that the faunal composition remains unchanged. However, as the ratios on different grounds with different faunas vary, a change in the faunal composition might alter the dry weight : wet weight ratio.

It has been shown that the series most nearly comparable to S is F2, both as regards faunal composition and bottom deposit. The biomass of the two grounds, however, is widely different. Table 7 gives the dry weights of animal matter on certain grounds together with carbon and phosphorus contents of the deposits. For the muddy sand deposits, S1 and F2, the greater biomass of S1 is accompanied by higher values of organic carbon and phosphorus. For the M sample, however, which was taken on the mud ground in about 50 fm depth outside the muddy sand area off Bradda Head, the carbon and phosphorus values are higher than at either

F2 or S1, although the biomass is lower. There is therefore no correlation between biomass and either carbon or phosphorus values for different grades of deposit.

On any of the types of ground investigated it seems unlikely that organic carbon can be a limiting factor in production. Taking the mean volume of 5·8 l.

Table 7. *Dry weights of animal matter and carbon and phosphorus content of certain deposits*

	Animals	Deposits	
Series	Dry wt./m²	Organic Carbon (%)	$\mu g PO_4'''$-P/g
S1	18·42	0·83	347
F2	2·71	0·40	295
M	2·11	0 98	471

of deposit taken per sample at F2, which when dried had a weight of about 8600 g, from the carbon value of the deposit there must be something like 34·5 g of carbon per 0·1 m² of deposit to a mean depth of 6 cm. The total dry weight of the animals present (macrofauna only) was 0·27 g /0·1 m². The amount of carbon in the deposit was therefore about 190 times as great as the total carbon in the macrofauna (taking the amount of carbon as 65% of the dry weight). In the case of S1 the ratio carbon in deposit : carbon in macrofauna was smaller (about 60 : 1) but a great excess of carbon was still present in the deposit. The figures are of the same order as those given by Mare (1942) for the Rame mud at Plymouth (100-200 : 1) Unless only a small fraction of the total carbon in the deposit is available for organic production it is difficult to see how the carbon content, even allowing for a rapid turnover by the microfauna, could limit production of animal tissue. It would in any case be limiting only to those animals feeding on the deposit itself, and could not affect suspension feeders. Taking the minimum figure of one-tenth of the organic carbon (Anderson 1939) as biologically utilizable the weight of animal matter nowhere approaches the limit set by this.

In the case of phosphorus there is about 2.5 g P per m² in the muddy sand deposit at F2 and 3·0 g m² at S1. Analyses of the dried animal matter gave the percentage of phosphorus as 0·297 and 0·420 for F2 and S1 respectively, so that the ratios of phosphorus in deposit : phosphorus in macrofauna were about 330 : 1 and 40 : 1. These values are widely different and again are much too high for phosphorus in the deposit to have any limiting effect.

The muddy sand fauna may be divided by feeding habit into groups according to the classification adopted by Blegvad (1914) and later by Hunt (1925) among others. The more important purely benthic forms (from p. 224) include about sixty-two species, and these make up more than 95% of the community both by number and weight. It might be expected that the majority of animals living on a soft bottom would be deposit feeders, and in this case they comprise more than 50% of the important species. Most of the lamellibranchs are suspension feeders, but this group includes only 18% of the total important species. The only group that is

directly dependent upon the organic matter in the deposit, as opposed to that which falls upon its surface, is the non-selective deposit feeders. These, however, comprise only about 6% of the total, and none of them is particularly abundant or of large size. All the rest are more or less directly dependent upon the plankton in the overlying water, either living or dead, in the case of carnivores through the intermediary of other members of the community, or upon small benthic forms living upon the surface of the deposit. It follows that the organic carbon or phosphorus content of the deposit can have little influence on the biomass of the benthos, and that no relation can be expected between them, except in so far as the organic contents of the deposit are a reflection of the nutrients in and plankton production of the overlying water. It is probable that where nutrient salts are abundant and the plankton crop rich, the underlying deposit will gradually become richer in organic matter, a great deal of this being locked up in the deposit, but the results of an analysis of the deposit are probably the reflection of past conditions in the overlying water rather than those existing at the time of the analysis. A deposit rich in organic matter might by exchange enrich the nutrients in the water when these become depleted, as Cooper (1951) has postulated for parts of the Celtic Sea, and in this way exert some effect on the biomass of the benthos. Over a long period this process might considerably reduce the organic content of the deposit if no new supply of nutrients was coming in from outside the area. Conversely the influx of nutrient-rich water into an area previously poorly supplied would probably in time increase the organic content of the deposits. The effect on the benthos would be more rapid, but in either mechanism there would be some delay between cause and effect. However, under fairly stable conditions it is reasonable to presume that a high or low organic content of the deposit is accompanied by a high or low biomass respectively, although the one is not the cause of the other and therefore cannot be a limiting factor.

At the nearest station to F2 at which water samples have been taken by Mr Slinn, the soluble phosphate content of the overlying water at the surface was: Sept.-Oct., 1954, 13 mg P/m^3; Nov.-Dec. 1954, 15 mg/m^3; June 1955, 14 mg/m^3. At the nearest station to S1 values were: Sept.-Oct. 1254, 13 mg/m^3; Nov.-Dec. 1954, 25 mg/m^3; June 1955, 5 mg/m^3. Although this evidence is far from conclusive it seems probable that the winter maximum of phosphorus is higher at S1 than at F2, while the lower values for S1 in June perhaps point to a greater phytoplankton production in that area compared with F2. If this is accompanied by a larger amount of zooplankton it could account for the higher biomass of the benthos at S1.

THE MUDDY SAND FAUNA AS A COMMUNITY

In a previous paper (Jones 1950) a scheme of classification of benthic marine communities was suggested, based finally on the nature of the bottom deposits. In this scheme, following Clements & Shelford (1939), the communities for each major type of deposit were described as biomes. According to Allee, Emerson *et al.* (1949) the whole of marine ecological associations constitutes essentially a single major

community and a single biome, because of the lack of effective barriers to dispersal, the slow continuous circulation of the medium, and the interdependence of its components from region to region and area to area. Although the biome is not exactly defined it is evident from the discussion of these authors that the marine benthic communities cannot be appropriately classified into biomes. Nevertheless the communities occurring on different types of bottom and in different regions are quite distinct entities, although some overlap occurs, and are both climatic and edaphic climaxes. It is true that they cannot be classified into biomes in the same way as the major communities on land, owing to the absence of discontinuity between them and to the relative uniformity of the water medium. As stated by Allee *et al.* pelagic animals may range over a very wide area, and since the benthic communities cannot be strictly separated from the over-lying plankton and nekton on which they are largely dependent, but which are less affected by the nature of the bottom, it is not possible to distinguish one from another as, for example, the African and American tropical forest biomes may be distinguished. However, even the plankton is very different in different parts of the ocean, and the fauna as a whole is temperature-limited almost to the same degree as the land fauna. It seems, therefore, stretching the biome concept too far to include the whole of the marine fauna and flora in a single biome. It is perhaps better to admit that the ocean cannot be compared ecologically with the land, and to apply the term biome only to the latter. The muddy sand fauna investigated here may be referred to simply as a community of the soft-bottom type. Hedgpeth (1954) emphasizes that the complex character of marine communities cannot be simplified by terminology.

The muddy sand contains a fauna recognizably distinct from those of deposits of different composition. The causes of this differentiation are partly physical and partly biological. The physical and chemical characteristics of the overlying water, so far as they are known, with the possible exception of depth, are so nearly uniform over the whole area that they are unlikely to cause any major differences in the composition of the benthos between one place and another. In the case of the bottom deposits, the chemical composition probably does not vary sufficiently to cause any considerable differences in the specific composition of the fauna, as opposed to the biomass. It seems to be the physical properties of the deposit that exert an appreciable effect. From the biological point of view food relationships are the most obvious causes of faunal differentiation.

The evidence that depth of water has any influence *per se* on the composition of the benthos is not great. Nevertheless Ford (1923) found that *Abra alba* occurred more commonly in shallow depths, while *A. prismatica* was more abundant in deeper water. In the present investigation *Abra alba* was found in about 10 fm off the Cumberland coast, where *A. prismatica* was scarce, while *A. prismatica* was abundant in depths of 30 fm or more off the Isle of Man, *A. alba* being apparently absent. The deposits from the two areas do not differ greatly. However, *A. prismatica* is also found in fine sand in water of about 10 fm depth in Port Erin Bay (Jones 1951), though less abundantly than on the muddy sand and mud, and there

is no obvious reason why the difference in pressure between 10 and 30 fm should affect the two species. It is possible that *Abra alba* is more tolerant of a lower salinity than is *A. prismatica*, and that this factor, rather than the depth of water, affects their distribution.

The effects of deposit grade upon the fauna can only be elucidated by observations and experiments upon individual species, such as those of Ekman (1947) and Yonge (1937, 1946). It is evident that the mechanical properties of the deposit largely determine which combination of particle size is most favourable to any species. Further experiments are also needed to assess the role of chemical and physical properties of the deposit or substratum on larval settlement, which have been shown by Wilson (1952) and others (see Thorson 1951, and Knight-Jones 1955) to be important.

THE ROLE OF FISH IN THE COMMUNITY

The role of fish in the muddy sand community is somewhat difficult to estimate. Some species of fish are present throughout the year and are benthic in habit, feeding on the invertebrates, and in fact must be considered as permanent members of the community. Others, while feeding on the bottom fauna, are more seasonal in occurrence, and may be abundant during one part of the year and scarce or absent during the remainder, having migrated into another area or into water of different depth. Nevertheless, while they are present they may exert a not inconsiderable influence on the community by eating up a proportion of the crop. Even the pelagic fish, although not directly affecting the benthos, must have some influence on it by feeding upon the plankton or upon other fish. The following list contains an approximate estimate of the mean catch of fish per hour duration with the otter trawl from *M.V. William Herdman* on the muddy sand ground (from figures kindly supplied by Mr A. B. Bowers of 27 hauls, including hauls with a fine-meshed cod end, for the period 1949-53):

Scyliorhinus caniculus	5	*Lepidorhombus whiff-iagonis*	5
Squalus acanthias	10	*Hippoglossoides platessoides*	5
Raja spp.	5	*Gadus callarias*	3
Trigla gurnardus	30	*G. aeglefinus*	5
T. cuculus	5	*G. merlangus*	60
T. lucerna	1	*G. luscus*	2
Microstomus kitt	2	*G. minutus*	30
Pleuronectes platessa	2	*G. esmarkii*	60
Limanda limanda	30	*Merluccius merluccius*	20
Glyptocephalus cynoglossus	30	*Argentina sphyraena*	50

Many of these fish range to some extent over neighbouring grounds. No figures are available to show any distinct seasonal variations in numbers, but on the whole fish are more abundant during the months February to May than at other times of the year. Cod, haddock and large whiting are caught in larger numbers during the spring and are usually scarce during the autumn and winter, while hake are caught mainly during the late spring and summer. The numbers of *Squalus* caught are very variable, more than 500 having been obtained in a single haul on occasions,

Table 8. *Food of fish on muddy sand ground off Port Erin, 1952-1953*

	Fish Species									
	1	2	3	4	5	6	7	8	9	10
	Trigla gurnardus	*Glyptocephalus cynoglossus*	*Lepidorhombus whiff-iagonis*	*Merluccius merluccius*	*Gadus callarias*	*Gadus aeglefinus*	*Gadus merlangus*	*Gadus minutus*	*Gadus esmarkii*	*Argentina sphyraena*
Number of full stomachs:	10	12	9	31	7	12	33	26	19	20
Aphrodite aculeata	—	—	—	—	—	—	—	2	1	—
Nephthys sp.	—	—	3	—	—	1	—	—	—	1
Glycera sp.	—	2	2	—	—	—	1	—	—	—
Goniada sp.	—	2	—	—	—	1	—	—	—	—
Lumbriconereis sp.	—	2	—	—	—	1	—	—	—	—
Spionid sp.	—	—	—	—	—	10	—	—	—	—
Pectinaria sp.	—	—	—	—	—	7	—	—	—	—
Notomastus latericeus	—	5	1	—	—	—	—	—	—	—
Ammotrypane aulogaster	—	2	—	—	—	—	—	—	—	—
Terebellid sp.	—	4	2	—	—	—	—	—	—	—
Unidentified polychaetes	—	—	—	—	—	2	—	2	—	1
Sagitta sp.	—	—	—	—	—	—	60+	—	—	30
Copepoda	—	1	—	—	—	—	1	40+	100+	2
Ostracoda	—	—	—	—	—	—	—	10+	—	—
Euphausid larvae	—	—	—	—	—	—	100+	65+	270+	100
Meganyctiphanes norvegica	—	—	—	—	—	—	1	—	—	—
Schistomysis ornata	—	—	—	1	—	—	1	—	—	—
Iphinoe serrata	—	—	—	—	—	8	—	—	—	1
Diastylis spp.	—	—	—	—	—	105+	—	1	—	1
Diastyloides biplicata	—	—	—	—	—	2	—	—	—	—
Cirolana borealis	—	—	9	—	—	—	7	1	1	—
Hippomedon denticulatus	—	—	—	—	—	—	1	—	—	—
Ampelisca spp.	1	6	4	—	—	65+	1	1	—	1
Harpinia sp.	—	—	—	—	—	1	—	2	—	—
Westwoodilla caecula	—	—	—	—	—	2	—	1	—	—
Unidentified amphipods	1	—	—	—	—	5	1	2	1	—
Pandalid sp.	—	—	—	1	—	—	8	—	—	—
Alphaeus ruber	1	—	1	—	—	1	9	10	—	—
Crangonid spp.	2	—	1	—	—	—	3	5	—	—
Processa canaliculata	7	—	1	—	—	—	1	—	—	—
Nephrops norvegicus	1	—	—	—	1	—	1	1	—	—
Anapagurus laevis	—	—	—	—	1	—	—	—	—	—
Galathea sp.	—	—	—	—	—	—	—	1	—	—
Portunus sp.	—	—	—	—	1	—	—	—	—	—
Hyas coarctatus	—	—	—	—	2	—	—	—	—	—
Unidentified decapods	—	—	1	1	7	1	1	—	1	—
Decapod larvae	85+	—	—	—	—	—	—	—	—	—
Dentalium entalis	—	—	—	—	1	—	—	—	—	—
Chlamys opercularis	—	—	—	—	1	—	—	—	—	—
Abra prismatica	—	—	5	—	—	25	—	—	—	—
Cultellus pellucidus	—	2	2	—	—	2	—	—	—	—
Cardium scabrum	—	—	—	—	—	100+	—	—	—	—
Hermania catena	—	1	—	—	—	—	—	—	—	—
Amphiura spp.	—	—	—	—	—	13	—	—	—	—
Ophiura sp.	—	—	—	—	—	1	1	—	—	—
Echinocyamus pusillus	—	—	—	—	—	6	—	—	—	—
Gadoids	1	—	—	23	2	—	3	—	—	—
Clupeids	—	—	—	2	—	—	—	—	—	—
Unidentified fish	12	—	3	8	2	2	3	—	—	—
Fish eggs	—	—	—	—	—	—	—	—	—	2
Fish larvae	—	—	—	—	—	—	—	—	4	—

particularly during the summer and early autumn when herring are present in large numbers. Other species of fish besides those listed are of occasional occurrence. From a commercial point of view the ground is seldom worth fishing, and is only visted by fishing vessels, mainly seine-netters, during the spring.

The results of the examination of the stomach contents of certain fish species caught on the muddy sand ground during 1952 and 1953 are shown in Table 8. For those species also examined by Steven (1930) the kind of food taken is very similar to that off Plymouth. On various occasions many fish were obtained with empty stomachs, but no attempt has been made to investigate seasonal changes in food. It is unlikely that there is much seasonal change with a stable bottom fauna apart from the usual reduction in the amount eaten during the winter months. Steven found little evidence of change off Plymouth.

For the smaller gadoids and for *Argentina* the important food organisms were largely planktonic in origin, including *Sagitta*, copepods and larval crustaceans. Amphipods, particularly *Ampelisca* spp., and cumaceans were eaten by the smaller species of fish. Decapods, of which *Alphaeus ruber* was the most important, were taken by most species. A number of species took polychaetes, especially *Nephthys* and the Glyceridae. Of the lamellibranchs *Abra prismatica*, *Cardium scabrum* and *Cultellus pellucidus* were most frequently eaten. *Amphiura* spp. were eaten to some extent by the smaller haddocks, while fish, where identified usually small gadoids, formed a substantial part of the food of the larger fishes. Only a very small number of the food organisms were not taken in the bottom samples, and the important species were among the most important elements of the bottom fauna. Taken as a whole it seems that little selection occurs, the more abundant constituents of the fauna being eaten to a greater extent than the less abundant, as might be expected. There are, however, species that are not eaten at all by fish, owing to their large size, hard exoskeleton, innaccessibility, or possibly distastefulness. Others do not appear among the stomach contents owing to the comparatively small number of stomachs examined and to their rarity in the fauna. The larger gastropods are not eaten for obvious reasons, while *Echinocardium*, though fragile enough to be broken into pieces of suitable size, is probably distasteful, perhaps because of its spines. *Corbula* is eaten only rarely, probably because it has a thick shell, but juvenile specimens may form part of the food of young fish. Although *Corbula* has other enemies, a proportion of those caught being empty and with the shell bored by a gastropod, probably *Natica poliana*, the abundance of adults of this species on the coarser muddy sand compared with other species of lamellibranchs may perhaps be explained by lack of predation by fish.

DATA ON LIFE-HISTORIES AND GROWTH

It is only possible in a synecological survey to obtain information on the growth-rates of the more abundant species, and where collections have to be preserved for later sorting and identification only on those with rigid skeletons or shells. In this investigation such information has been obtained only for some of the Mollusca and Echinodermata.

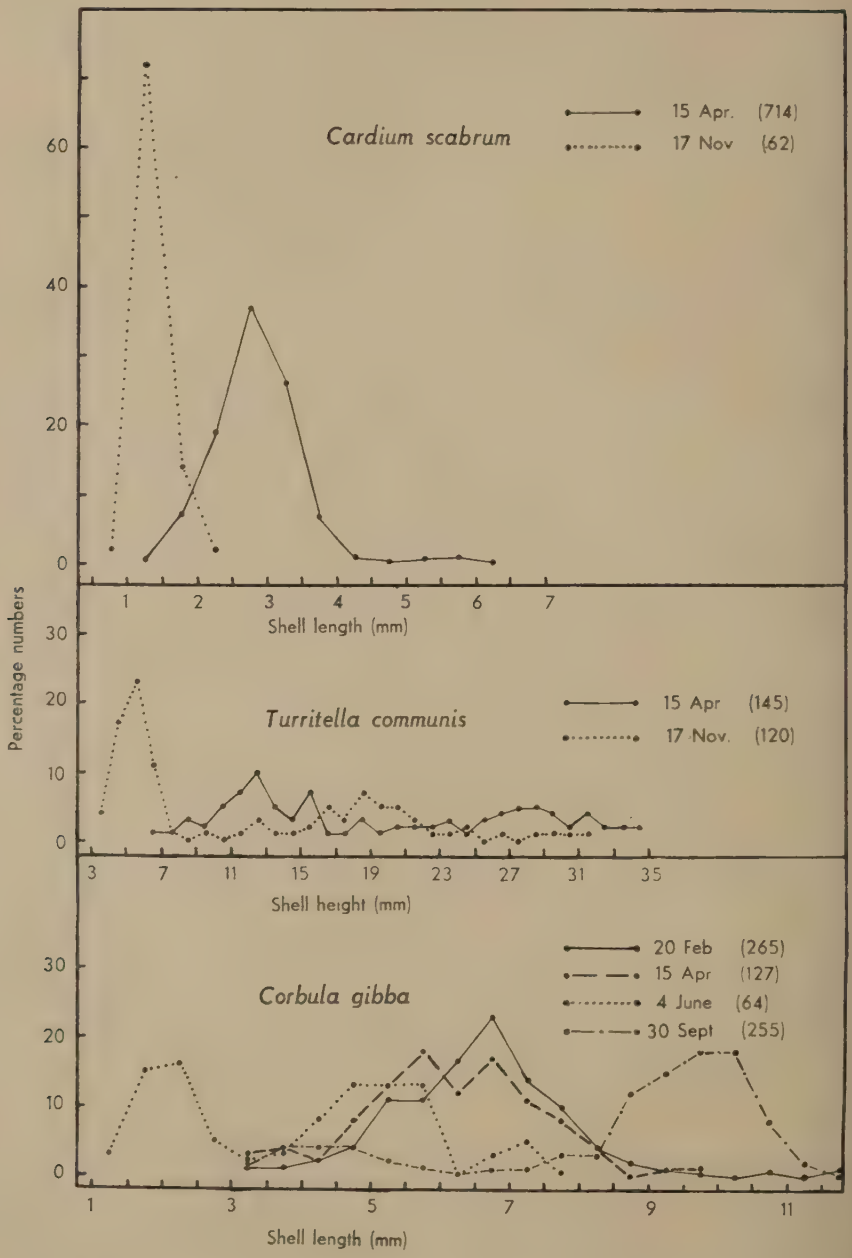


Fig. 3. Size distribution curves for samples of *Cardium scabrum*, *Turritella communis* and *Corbula gibba*. Total numbers in each sample are shown in parentheses.

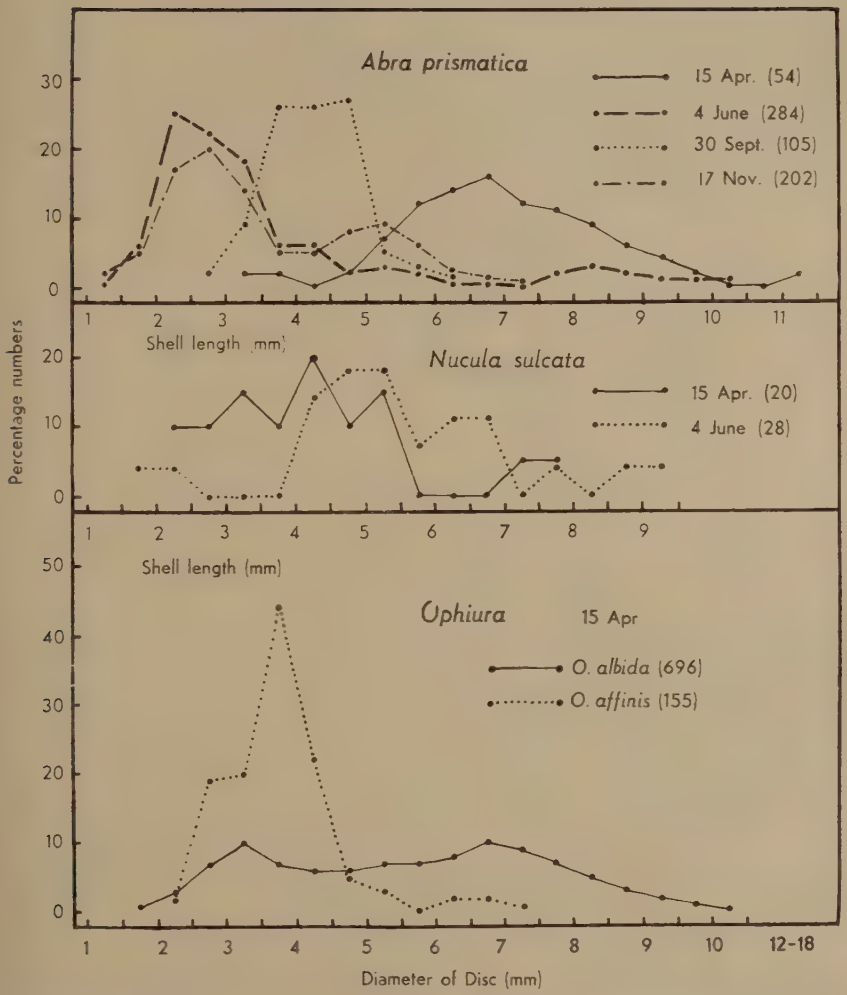


Fig. 4. Size distribution curves for *Abra prismatica*, *Nucula sulcata*, *Ophiura albida* and *O. affinis*.

Size distributions for some of the species that were obtained in sufficient numbers are shown in Figs. 3 and 4. From these certain conclusions may be drawn. The curves for *Cardium scabrum* contrast strongly with those for *Turritella communis*. *Cardium scabrum* is relatively soft-shelled and is taken in large numbers by fish, especially small haddocks, so that a heavy spatfall is soon reduced. Few large specimens occur, and it seems from the size distribution on 15 April that individuals seldom survive into the second year. In a runner-dredge haul taken two months later on 4 June only one specimen was obtained. Seven months after this, however, on 17 November, a fresh spatfall had occurred, presumably in the autumn, as numerous specimens were obtained with a length of only 1-2 mm. It

Fig. 5. Growth curve for *Corbula gibba*.

does not follow that the failure of *C. scabrum* to reach the age of more than one year after settlement is due to the feeding of fish upon them, although this is almost certainly a contributory cause. *C. scabrum* may in any event be largely an annual species, each individual dying after the reproductive cycle is completed. It is possible, however, if this is the case, that the species has become an annual by the action of selection through the agency of depredations by fish. *Turritella communis*, on the other hand, has a thick shell and grows to a large size. It is rarely eaten, only a few specimens having been found in the stomachs of large cod. The species shows no sign of a great decrease in numbers after the first year and evidently many specimens survive for a number of years.

The size distribution curves for *Abra prismatica* and *Ophiura affinis* are similar in form to those for *Cardium scabrum*, while those for *Nucula sulcata* and *Ophiura albida* show more resemblance to those for *Turritella communis*. *Abra prismatica* is eaten by a number of species of fish, though the numbers do not seem to be reduced so catastrophically as in *Cardium scabrum*, and a fair number live into the second year and beyond. It would appear from the size distribution of *Abra prismatica* that during 1952 there were two main spatfalls, one during the spring and the second in the late summer or autumn. That the species normally has two breeding periods per year in the North Sea is shown to be probable by Rees (1954) from the occurrence of the larvae. *Nucula sulcata*, being thick-shelled, rarely

appears among stomach contents. *Ophiura affinis* is less heavily calcified than *O. albida* and is probably eaten in preference to the latter, although neither is taken to such a large extent as the thin-shelled lamellibranchs.

By plotting the peaks in the curves for *Corbula gibba* against time it is possible to produce an approximate growth curve (Fig. 5). It seems likely from this that the species may reach an age of at least four years after settlement. The larvae were found in the plankton off Helsingør, Denmark, mainly in September and October, but some in winter and spring (Jørgensen in Thorson 1946). They must have settled off the Isle of Man during 1952 in the early spring since a number

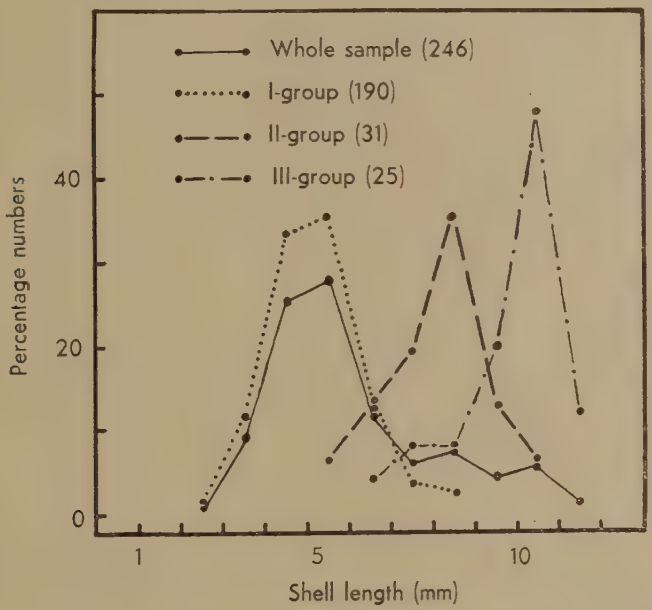


Fig. 6. Size distribution curves for sample of *Corbula gibba* taken on 17 April 1950.

were found in June with a modal length of 2·25 mm, while none as small as this was found earlier in the year. The growth curve is supported by the size distribution of a sample of 246 taken on the same ground on 17 April 1950. It is possible in most cases to distinguish growth rings on the shell. The modal sizes of specimens with 1, 2 and 3 rings respectively corresponded with the modes in the curve for the whole collection (Fig. 6), and were presumably representative of groups 1, 2 and 3 years of age after settlement. Caspers (1950) found a modal size among eighty-two specimens at Heligoland of 4 mm in October, which is not inconsistent with their growth off Port Erin.

CONCLUSIONS

The results of the investigations detailed in this paper make it clear that for understanding the causes of differences in animal production on the sea bottom there is little to be gained by comparing one area with another. This may perhaps be useful on broad lines from a zoogeographical aspect or from the point of view of the distribution of fishes as especially undertaken by Russian workers (Zenkewitsch 1947), but the great variation found to occur within a small linear distance, correlated with a change in the mean size of particle in the deposit, prevents any precise conclusions from a comparison of the biomass in different places: to be of value comparisons must be made between places with exactly similar deposits, and the chances of such being encountered are slight. The detailed comparison of the production at a single location over a period of time is more promising provided that certain precautions are taken: it should be possible to locate the position within a small margin of error whenever desired: it would be preferable to choose a position in the centre of a fairly large area with a similar deposit, and to check periodically that the deposit does not change: a deposit should be chosen that is soft enough to give reliable results with a bottom-sampler, at least twenty samples should be taken at each station, and the same method adopted throughout the work. Such an investigation would necessarily be prolonged over many years, and would probably have more chance of success if carried out in an area such as the English Channel where it is known that there have been changes in the water masses, and where it might be expected that further changes would take place. It would be necessary to eliminate local alterations due purely to chance, as might be the case in variations of biomass due to the successful or unsuccessful settlement of the larvae of one or more species: on the other hand such variations might be correlated with measurable changes in the environment. It would be advisable to measure not only total dry weights for each sample, but also dry weights separately of all the species present in considerable numbers, so that a statistical check could be kept on individual species, any of which might provide better evidence than the whole.

The only environmental factor so far examined with which changes in the biomass of the benthos may be correlated (where temperature, salinity and grade of deposit remain stable) seems to be the concentration of phosphorus in the overlying water. The results in this paper do not disprove this possibility, and other evidence suggests that it may exist. At the same time the presence of certain species in the plankton only in certain water masses points to some unknown factor involved in the control of distribution, since the phosphorus content of different water masses may be similar, and although such indicator species are unknown among the benthos, the experiments of Wilson on the settlement of *Ophelia* larvae show that a change in the composition of the benthos might be the result of an alteration in the concentration of some factor other than phosphorus. Such a change might not affect the biomass but the possibility should be borne in mind.

ACKNOWLEDGMENTS

I am much indebted to Mr D. J. Slinn for the time and care which he has bestowed on the chemical analyses included in this paper, and for information concerning the distribution of phosphates in the area. Some of the Polychaeta were kindly identified for me by Mrs E. C. Southward.

SUMMARY

1. Five series of samples with a 0·1 m² van Veen grab and a number of runner-dredge hauls were taken at intervals of 2-3 months during 1952 in an area of muddy sand centred 7 miles N-W of Port Erin. Little seasonal variation occurred in the fauna, but a small change in position could be accompanied by a large alteration in faunal composition and biomass.

2. Three further series taken in June 1953 showed significant differences in the numbers of *Corbula gibba* between 1952 and 1953. The coarse muddy sand off Port Erin supported a much richer fauna with a higher biomass than the finer deposits only ½ mile seawards. The series taken off the Cumberland coast showed little change after an interval of three years and the biomass was much higher than on the fine muddy sand ground off Port Erin.

3. For reliable biomass estimations twenty samples at each station are desirable.

4. There is no correlation between dry weights of the fauna at several stations and the organic carbon and total phosphorus contents of the deposits. The ratios of carbon and phosphorus in the macrofauna to the same in the deposits are much too large for the carbon or phosphorus to be limiting to the biomass. It is possible that total phosphorus in the overlying water is limiting.

5. It is suggested that the term biome is not applicable to the marine fauna and flora.

6. The role of fish in the muddy sand community is briefly discussed, and data are given on the feeding of certain species.

7. *Cardium scabrum* appears to be an annual and *Abra prismatica* to have two breeding periods per year. A growth curve is constructed for *Corbula gibba*.

8. Methods of chemical analysis of organic carbon and total phosphorus in deposits and dried animal remains are outlined in an appendix.

APPENDIX

METHODS USED FOR THE ANALYSIS OF DEPOSITS AND ANIMAL MATERIAL

By D. J. SLINN

Organic carbon was estimated by the chromic acid method, the modification of Schollenberger (1927) by Allison (1935) being adopted. The dried deposit is finely ground in a mortar and 0·5000 g samples weighed out. These are then

c

heated in a boiling tube with potassium dichromate (0·1961 g) and concentrated sulphuric acid (10 ml). The temperature is allowed to rise steadily to about 175° C, after which heating is discontinued. The tube is cooled in air for about 5 min, and then in running tap water. The contents are poured into cold water and the excess potassium dichromate titrated against a standard (0·2 N) ferrous ammonium sulphate solution using diphenylamine as an indicator. Now 1 ml 0·2 N ferrous ammonium sulphate = 0.009807 g potassium dichromate = 0.0006 g carbon, so that if recovery is 100% and 0.5000 g samples are taken, the theoretical carbon factor is (0·0006 × 100) 0·5 = 0·12% for each ml of 0.2 N ferrous ammonium sulphate.

Under the experimental conditions, however, oxidation of the organic carbon is fairly uniformly incomplete (a mean value of 86·9%) so that the theoretical carbon factor has to be modified to (0·12 × 100) 86·9 − 0·138% (for each ml of 0·2 N ferrous ammonium sulphate). A blank determination is also run off—the above procedure is repeated without the addition of a mud sample. With 0·2 N ferrous ammonium sulphate and 0·1961 g potassium dichromate the burette reading should be 20·00 ml. If it differs from this then the corresponding organic factor is given by (20·00 × 0·138)/ml blank %

Results:

Sample	Mean organic carbon (%)	Number of estimations	Standard deviation
F2	0·401	12	0·043
S1	0·826	10	0·029
M	0·982	2	—

This method assumes that only organic carbon will reduce the potassium dichromate. Southward (1952), however, has pointed out that other substances which will react with the potassium dichromate under the experimental conditions may be present in certain marine deposits. Such substances include coal (originally assumed to be inert) and reducing agents such as ferrous iron. The samples were examined microscopically for coal fragments but only traces were found (probably insufficient to affect the final result). As yet there is no method to correct for this coal error.

Total ferrous iron is rather difficult to estimate, but we are only concerned here with that likely to reduce potassium dichromate under the experimental conditions. Consistent results were obtained between duplicates by extracting weighed samples (1·0000 g) of the dried and powdered deposit with boiling 10% sulphuric acid in a stream of carbon dioxide. After 2-3 min the mixture was filtered (No. 2 Whatman) and the filtrate made up to a known volume. The ferrous iron content of this extract was determined colorimetrically in a 'Spekker' absorbtiometer, two methods being tried:

(*a*) Estimation of the original Fe^{+++} by thiocyanate, followed by oxidation and re-estimation of Fe^{+++}, the difference being equivalent to Fe^{++}. The thiocyanate method is fairly straightforward and the estimation may be carried out in a strongly acid solution. There are, however, several disadvantages, notably the fading of

colour with time, and the interference of such ions as fluoride, metaphosphate and pyrophosphate which form complexes with ferric iron in acid solution. Sulphate ions also depress the colour intensity, but if equivalent amounts of sulphuric acid are added to the standards this difficulty may be minimized. Hydrochloric or nitric acids are normally used in this determination, but Thompson, Bremner & Jamieson (1932) have pointed out that alkali earth chlorides interfere with the colour formation, and for this reason hydrochloric acid was not used. Nitric acid was rejected since it might oxidize some of the Fe^{++}. By using a high thiocyanate concentration, the colour of the complex can be stabilized, and also the effect of interfering substances reduced. The rate of fading of the colour was found to be much less than expected, and since estimations were carried out within a few minutes of adding the thiocyanate, it is thought that little error may have resulted from this cause. Several oxidizing agents were tried, and boiling with potassium permanganate (in acid solution) was found to give the most consistent results. The excess permanganate may be decolorized with hydrogen peroxide, and in this connection it may be noted that Houlihan & Farina (1953) recommend the addition of a few drops of concentrated hydrogen peroxide to stabilize the colour of the thiocyanate complex. However, they used a relatively low thiocyanate concentration, since at higher concentrations a deep yellow coloration may be produced with hydrogen peroxide. A calibration curve was constructed using a standard iron (ferric alum *A.R.*) solution.

(*b*) Fe^{++} in the extract (prepared as described above) was estimated directly using α, α′-dipyridyl (see Cooper 1935, 1948*a*) after ensuring that the pH was within the range (pH 3·5-8·5) for the stable formation of the deep red co-ordination compound. A calibration curve was constructed by suitable increments of a standard ferric alum solution.

Cooper (1948*c*) notes that at high dilutions ferric iron can react with dipyridyl to give the red ferrous complex. Schnitzer & Delong (1954) obtained abnormally high results by the application of the dipyridyl method to a system containing Fe^{+++}, Fe^{++} and oxidizable organic matter. They suggested the explanation might be, that removal of Fe^{++} by dipyridyl increases the oxidation potential of $Fe^{+++} \rightarrow Fe^{++}$ thus favouring further oxidation of organic matter and subsequent reduction of Fe^{+++}. In the analyses performed on the present samples, the results obtained by using dipyridyl do not differ markedly from those obtained with thiocyanate, although it may be noted that those for sample M are slightly higher, and that it is this sample which contains the highest percentage of organic carbon.

Results:

Sample	By thiocyanate			By α, α′-dipyridyl		
	Number of estimations	Mean Fe^{++} mg/g	Standard deviation	Number of estimations	Mean Fe^{++} mg/g	Standard deviation
M	2	6·6	—	2	7·8	—
F2	8	4·0	0·36	10	3·1	0·10
S1	—	—	—	10	4·0	0·57

Now 1 g Fe^{++} ≡ 0·05372 g carbon, and the following table shows the reducing power of the ferrous iron content of the samples in terms of organic carbon:

	Fe^{++} content ≡ mg carbon	
Sample	By thiocyanate	By α, α′-dipyridyl
M	0·042	0·036
F2	0·021	0·017
S1	—	0·021

It is seen that in both F2 and S1 samples ferrous iron is present in amount equivalent to 0·02% organic carbon, and that in the M sample it is present in amount equivalent to 0·04% organic carbon. Both these results are within the experimental error recorded earlier.

Total phosphorus was estimated according to a method proposed by Dr J. P. Riley (Department of Oceanography, Liverpool) and to be published elsewhere. Concentrated nitric acid and perchloric acid are used to bring the phosphorus into solution as phosphate. This is then estimated by reduction of phosphomolybdic acid with stannous chloride to form a blue complex, the optical density of which is measured colorimetrically (see e.g. Harvey 1948, Armstrong 1949, Watson & Rakestraw 1951). A calibration curve may be constructed or the phosphate content determined by increment. The latter method, though perhaps more time-consuming than the former, was suggested because interfering substances which tended to depress the intensity of the blue coloration, were sometimes present.

Results:

	Means expressed as μg $PO_4^{\cdots}$ –P/g mud					
	By Calibration Curve			By Increment		
Sample	Mean $PO_4^{\cdots}$ –P	Number of estimations	Standard deviation	Mean $PO_4^{\cdots}$ –P	Number of estimations	Standard deviation
S1	342	14	7·0	347	10	9·4
F2	295	10	10·7	295	10	10·5
M	453	2	—	471	2	—

The total phosphorus content of some dried animal material from the same areas as the deposit samples was also estimated. The procedure adopted was much the same as that described above, except that a preliminary digestion with concentrated nitric acid on a water bath was found to be necessary to oxidize the excess organic material.

Results:

	Means expressed as mg $PO_4^{\cdots}$ –P/g dried material					
	By Calibration Curve			By Increment		
Sample	Mean $PO_4^{\cdots}$ –P	Number of estimations	Standard deviation	Mean $PO_4^{\cdots}$ –P	Number of estimations	Standard deviation
S1	4·45	4	0·10	4·20	4	0·10
F1	2·75	2	—	2·75	2	—
F2	3·12	1	—	2·97	1	—

REFERENCES

Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). *Principles of Animal Ecology.* Philadelphia.

Allison, L. E. (1935). Organic soil carbon by reduction of chromic acid. *Soil Sci.* **40,** 311-20.

Anderson, D. Q. 1939. Distribution of organic matter in marine sediments and its availability to further decomposition. *J. Mar. Res.* **2,** 225-35.

Armstrong, F. A. J. (1949). A source of error in the absorbtiometric determination of inorganic and total phosphorus in sea water. *J. Mar. Biol. Ass. U.K.* **28,** 701-5.

Armstrong, F. A. J. & Harvey, H. W. (1950). The cycle of phosphorus in the waters of the English Channel. *J. Mar. Biol. Ass. U.K.* **29,** 145-62.

Blegvad, H. 1914. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. *Rep. Danish Biol. Sta.* **22,** 43-78.

Blegvad, H. 1925. Continued studies on the quantity of fish food in the sea bottom. *Rep. Danish Biol. Sta.* **31,** 27-56.

Caspers, H. 1950. Die Lebensgemeinschaft der Helgoländer Austernbank. *Helgoländ, wiss. Meeresunters.* **3,** 119-69.

Clements, F. E. & Shelford, V. E. (1939). *Bio-Ecology.* New York.

Cooper, L. H. N. 1935. Iron in the sea and in marine plankton. *Proc. Roy. Soc.* (B) **118,** 419-38.

Cooper, L. H. N. 1948a. The distribution of iron in the waters of the western English Channel. *J. Mar. Biol. Ass. U.K.* **27,** 279-313.

Cooper, L. H. N. 1948b. Phosphate and fisheries. *J. Mar. Biol. Ass. U.K.* **27,** 326-36.

Cooper, L. H. N. 1948c. Some chemical considerations on the distribution of iron in the sea. *J. Mar. Biol. Ass. U.K.* **27,** 314-21.

Cooper, L. H. N. 1951. Chemical properties of the sea water in the neighbourhood of the Labadie Bank. *J. Mar. Biol. Ass. U.K.* **30,** 21-6.

Ekman, S. (1947). Über die Festigkeit der marinen Sedimente als Faktor der Tierverbreitung, ein Beitrag zur Associations-analyse. *Zool. Bidr. Uppsala,* **25,** 1-20.

Ford, E. 1923. Animal communities of the level sea-bottom in the waters adjacent to Plymouth. *J. Mar. Biol. Ass. U.K.* **13,** 164-224.

Harvey, H. W. (1948). The estimation of phosphate and of total phosphorus in sea waters. *J. Mar. Biol. Ass. U.K.* **27,** 337-59.

Harvey, H. W. 1950. On the production of living matter in the sea off Plymouth. *J. Mar. Biol. Ass. U.K.* **29,** 97-138.

Hedgpeth, J. W. 1954. Bottom communities of the Gulf of Mexico. *Fish. Bull. U.S.* **55,** 203-14.

Holme, N. A. 1953. The biomass of the bottom fauna in the English Channel off Plymouth. *J. Mar. Biol. Ass. U.K.* **32,** 1-49.

Houlihan, J. E. & Farina, P. E. L. (1953). The thiocyanate determination of iron with hydrogen peroxide. *Analyst,* **78,** 559.

Hunt, O. D. (1925). The food of the bottom fauna of the Plymouth fishing grounds. *J. Mar. Biol. Ass. U.K.* **13,** 560-99.

Jones, N. S. 1950. Marine bottom communities. *Biol. Rev.* **25,** 283-313.

Jones, N. S. (1951). The bottom fauna off the south of the Isle of Man. *J. Anim. Ecol.* **20,** 132-44.

Jones, N. S. (1952). The bottom fauna and the food of flatfish off the Cumberland coast. *J. Anim. Ecol.* **21,** 182-205.

Knight-Jones, E. W. (1955). The gregarious setting reaction of barnacles as a measure of systematic affinity. *Nature, Lond.* **175,** 266.

Mare, M. F. (1942). A study of a marine benthic community with special reference to the micro-organisms. *J. Mar. Biol. Ass. U.K.* **25,** 517-54.

Raymont, J. E. G. (1950). A fish cultivation experiment in an arm of a sea loch. IV. The bottom fauna of Kyle Scotnish. *Proc. Roy. Soc. Edinb.* (B) **64,** 65-108.

Rees, C. B. 1954. The distribution of lamellibranch larvae in the North Sea, 1950-51. *Bull. Mar. Ecol.* **4,** 21-46.

Schnitzer, M. & Delong, W. A. (1954). Notes on the reaction of 2,2'-Dipyridyl with Iron in the presence of organic matter. *Canad. J. Agric. Sci.* **34,** 324-5.

Schollenberger, C. J. 1927). A rapid approximate method for determining soil organic matter. *Soil Sci.* **24,** 65-8.

Southward, A. J. (1952). Organic matter in littoral deposits. *Nature, Lond.* **169** 888.

Steven, G. A. 1930 . Bottom fauna and the food of fishes. *J. Mar. Biol. Ass. U.K.* **16,** 677-705.

Thompson, T. G., Bremner, R. W. & Jamieson, I. M. 1932 . Occurrence and determination of iron in sea water. *Indust. Engng. Chem., Anal. Ed.* **4,** 288-94.

Thorson, G. 1946 . Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Havundersøg. Kbh. Ser. Plankton* **4,** 5-523.

Thorson, G. 1951 . Zur jetzigen Lage der marinen Bodentier-Ökologie. *Verh. dtsch. zool. Ges., Wilhelmshaven,* 1951, 276-327.

Ursin, E. 1954 . Efficiency of marine bottom samplers of the van Veen and Petersen types. *Medd. Komm. Havundersøg. Kbh.* (n.s.) **1,** 1-8.

Wilson, D. P. 1952 . The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. *Ann. Inst. océanogr., Monaco,* **27,** 49-156.

Wooster, W. S. & Rakestraw, N. W. 1951 . The estimation of dissolved phosphate in sea water. *J. Mar. Res.* **10,** 91-100.

Yonge, C. M. 1937 . The biology of *Aporrhais pes-pelecani* L. and *A. serresiana* Mich. *J. Mar. Biol. Ass. U.K.* **21,** 687-704.

Yonge, C. M. 1946 . On the habits of *Turritella communis* Risso. *J. Mar. Biol. Ass. U.K.* **26,** 377-80.

Zenkewitsch, L. A. 1947 . *Fauna i biologicheskaia produktivnost' morya.* Leningrad.

STATISTICS OF THE BRITISH POPULATION OF THE PINK-FOOTED GOOSE

By H. BOYD

Wildfowl Trust, Slimbridge, Gloucestershire

It is remarkable that, despite the concern about the number of wildfowl expressed by many people with varied interests, little is known about the changes in numbers of any species in Britain, or about the relative importance of the various factors supposed to produce these changes. The objects of the study of the pink-footed goose (*Anser brachyrynchus*) begun by the Wildfowl Trust in 1950 were first to discover as much as possible about the characteristics of the British population of that species, and second to explore and improve the methods available for the study of wildfowl populations in general. The pinkfoot seemed the most suitable species of goose for the purpose of a preliminary investigation because, it seemed possible to define the population being studied with unusual precision because its breeding range was known and its breeding colonies were more accessible than those of any other British goose, and because its winter feeding habits made it relatively easy to catch.

Little needs to be said here about the sources of the data on which this report is based. They were obtained from the capture of geese in Britain each autumn from 1950 to 1954 (a total of over 5500), using rocket-propelled nets (the method is described in the Fifth Annual Report of the Wildfowl Trust) and from catches made during two expeditions to a large breeding colony in central Iceland in 1951 (1150 caught) and 1953 (9000 caught). The 1951 Iceland expedition was described by Scott, Fisher & Guðmundsson (1953) and by Scott & Fisher (1953). An account of the 1953 expedition is given by Scott, Boyd & Sladen (1955).

THE BRITISH POPULATION

The pink-footed goose breeds in Greenland, Iceland and Spitzbergen. Between mid-September and early May it is found in large numbers in Scotland, England and Wales, Denmark, Germany and Holland. There are records from several other countries, but these do not include regular occurrences of considerable numbers. The sampling to be discussed here was done in Scotland and England, very largely in the months of October and November. Consequently, it can only yield estimates of the total numbers of the species if geese from all three breeding areas are equally liable to capture in Britain in those months. From recoveries of ringed birds it seems unlikely that this condition is fulfilled. The geese breeding in central Iceland are almost wholly concentrated in Britain in October and November. In 1951-53 there were 249 recoveries and 200 recaptures of Iceland-ringed birds in Scotland and England in those months, compared with only one recovery

from Denmark, one from Holland and none from Germany. No pinkfeet have been ringed in Greenland, but three British-ringed and three Iceland-ringed birds have been shot there, so that some part of the Greenland population certainly visits Britain and there is evidently some mixing of the Iceland and Greenland birds. There have been no recoveries in Spitzbergen of birds ringed in Britain. One British-ringed pinkfoot has been found in Denmark (December 1953), but so far none in Germany. Recoveries from 567 pinkfeet ringed in Spitzbergen in 1952 and 1954 have come mainly from Denmark and Germany, also from Holland, Belgium and France, but not from Britain (Goodhart, Webbe & Wright 1955). It seems unlikely that the Spitzbergen population contributes materially to the numbers present in Britain in autumn. The population discussed in this paper is, except where otherwise stated, the British population, defined as the pinkfeet visiting Britain in autumn or, alternatively, the pinkfeet breeding in Iceland and Greenland together with those of their offspring surviving until the completion of their first southward migration.

ADULT MORTALITY

(*a*) *Causes of death*

Before discussing the death-rate of pinkfeet and methods for its determination it is appropriate to consider the causes of death and how these affect different classes, particularly different age-classes, in the population. It is convenient to begin by considering the death-rate of geese after fledging, that is from the time they enter the British population. The investigation of losses before fledging and in the first migration requires the use of different data and techniques. These are described in Scott, Boyd & Sladen (1955).

The data on the causes of death of pinkfeet after fledging consist almost entirely of reports concerning ringed birds. More than 1000 such reports were made between October 1950 and July 1954. Some of them give no details at all of the way in which the ring was obtained. When these are discarded 982 remain. In at least 860 cases (88%) the cause of death was shooting. Most of the other 122 have been 'found dead', in many cases so damaged, or so long dead, that the cause of death was not apparent. A number of these were probably also shooting casualties. Twelve birds were found dead, or too damaged to fly, after collisions with telegraph wires or high-tension cables. Two had apparently died after becoming oiled. Thus not less that 89% of the reported casualties were attributable to human activities. This does not mean that only 11% of adult pinkfeet losses are due to 'natural causes', because it must be presumed that the chance of a bird dying naturally being found and reported is less than that of a bird killed by man. But it suggests that man is the principal cause of adult losses and that the study of the distribution of the recoveries of marked birds may provide a satisfactory representation of the incidence of mortality amongst fledged pinkfeet. Hickey (1952) has provided a hopeful general discussion of the validity of using shooting recoveries for the determination of mortality rates to which the sceptical are referred. No treatment of natural mortality is yet possible.

(b) Estimation of the death-rate from recoveries

Both recoveries of dead birds and recaptures can be used for estimating death-rates. Recoveries are more useful, because much more numerous. Recoveries of geese marked from 1950-52 are set out in Table 1; geese marked in 1953 and 1954 are omitted since they have not yet been at risk for more than one year; birds marked as juveniles or goslings are tabulated separately, since it has already been shown (Boyd 1953) that mortality in the first year of life is greater than that in subsequent years, making it desirable to compute death-rates for the two classes separately.

Table 1. *Numbers of ringed pink-footed geese recovered 1953-54, with models for the estimation of adult and juvenile death-rates*

Year: 1 November-31 October. d = probability of dying during a year, $e(=1-d)$ = survival-rate, λ = reporting-rate.

Date of marking	Number released	Recovered in 1950-51	1951-52	1952-53	1953-54	Unaccounted for
ADULTS WHEN MARKED						
Autumn 1950	301	32	22	16	7	224
Autumn 1951	766		70	50	9	637
Autumn 1952	897			52	29	816
Probabilities		λd	$\lambda_1 e d$	$\lambda_2 e^2 d$	$\lambda_3 e^3 d$	$(1-\lambda d-\lambda_1 e d-\lambda_2 e^2 d-\lambda_3 e^3 d)$
			$\lambda_1 d$	$\lambda_2 e d$	$\lambda_3 e^2 d$	$(1-\lambda_1 d-\lambda_2 e d-\lambda_3 e^2 d)$
				$\lambda_2 d$	$\lambda_3 e d$	$(1-\lambda_2 d-\lambda_3 e d)$
GOSLINGS AND JUVENILES WHEN MARKED						
Autumn 1950	252	30	18	9	2	193
*Summer 1951	769		87	18	2	662
Autumn 1951	141		14	8	4	115
Autumn 1952	225			30	5	190
Probabilities		λd_1	$\lambda_1 e_1 d$	$\lambda_2 e_1 e d$	$\lambda_3 e_1 e^2 d$	$(1-\lambda d_1-\lambda_1 e_1 d-\lambda_2 e_1 e d-\lambda_3 e_1 e^2 d)$
			$\pi\lambda_1 d_1$	$\pi\lambda_2 e_1 d$	$\pi\lambda_3 e_1 e d$	$(1-\pi\lambda_1 d_1-\pi\lambda_2 e_1 d-\pi\lambda_3 e_1 e d)$
			$\lambda_1 d_1$	$\lambda_2 e_1 d$	$\lambda_3 e_1 e d$	$(1-\lambda_1 d_1-\lambda_2 e_1 d-\lambda_3 e_1 e d)$
				$\lambda_2 d_1$	$\lambda_3 e_1 d$	$(1-\lambda_2 d_1-\lambda_3 e_1 d)$

* Goslings marked in Iceland. The adult catches in Britain and Iceland in 1951 have been lumped together on the assumption (not contradicted by the data) that the adult death-rate between July and September is negligible. The death-rate of goslings during this interval is not negligible and a factor π, the survival-rate, is therefore included in the juvenile probability table.

There is a major difficulty in using recoveries. These are not the numbers of marked birds dying in a given time-interval but only that proportion of the losses which happens to be reported. This proportion has apparently fallen with the years (Table 2). The recovery figures do not in themselves indicate whether this is because of a declining death-rate, the reporting-rate remaining constant, or whether

the reporting-rate has fallen while the death-rate has remained approximately constant. But there are other grounds for supposing the second alternative to be more likely. Most of the recoveries are due to shooting. This study has been regarded with increasing suspicion or hostility by some wildfowlers, and some recoveries of ringed birds have been deliberately withheld. Other wildfowlers have evidently felt that if they have returned one ring any others found by them are of little interest. And from a study of the letters reporting recoveries it is apparent that in most areas the kill in 1953-54 was large, in contradiction to the implication of the reduced proportion of recoveries reported in that season. Thus in the treatment which follows the first hypothesis is preferred, but a method of calculation incorporating the assumption of a varying death-rate with constant reporting-rate is also shown.

Table 2. *Recovery-rates of October-ringed pink-footed geese in season of marking*

	Number of adults marked	Adults recovered (%)	Number of juveniles marked	Juveniles recovered (%)	Total recoveries (%)
1950	200	11·0	170	14·1	12·4
1951	384	9·1	141	9·9	9·3
1952	434	6·2	118	15·3	8·1
1953	577	6·2	294	4·4	5·6

Table 1, besides recording the numbers of recoveries in each year, tabulates the probability of a marked goose appearing in any class in the table, on the assumption that the adult death-rate d is constant from year to year and is independent of age. The juvenile death-rate d', is assumed different from d, but also constant are estimated from the observed numbers of recoveries and their expected values from year to year. The death-rates, and the annual reporting-rates (λ, λ_1, λ_2, λ_3),

Table 3. *Numbers of adult and juvenile pinkfeet in British catches 1950-54*

The 1954 totals are recorded separately because they were not used in the calculation of the death-rate from the recoveries of geese marked in 1950-52.

	1950	1951	1952	1953	Total 1950-53	1954	Total
Adults	307	387	907	1052	2653	1049	3702
Juveniles	257	143	226	506	1132	510	1642
Total	564	530	1133	1558	3785	1559	5344
Juveniles (%)	45·6	27·0	19·9	32·5	29·9	32·7	30·7

by the method of maximum-likelihood of Fisher (1954). By themselves, the recovery figures permit the estimation of the relative values of the death-rates and reporting-rates, but not of their absolute values, since, as has been noted, there can be no real discrimination between a low death-rate with a high proportion of recoveries and a high death-rate with a correspondingly low proportion of recoveries. Thus the estimation of d and of λ_1, λ_2, λ_3, must depend on the allotment of an arbitrary value to λ (the reporting-rate in 1950-51) unless some independent method of determining the relation between recovery and reporting can be found. This can be done by making use of the juvenile : adult ratios in the British autumn catches (Table 3) to provide information on the ratio occurring in the whole population.

In a stable population, it is possible to express the numbers in each age-group in terms of the (constant) birth- and death-rates, and so estimate these rates from the juvenile : adult ratio. However, the variation between years of this ratio (in the catches) is larger than that between catches in different places in the same year, which is itself very much larger than might be expected theoretically. (The values of χ^2 are 127 (3 degrees of freedom) and 198 (20 d.f.), giving a variance of 4·3.) It is, therefore, necessary to allow for variation in the numbers of juveniles in different years. It may be argued that, since there is such a large variation in the juvenile : adult ratio between different catches any attempt at estimation should be abandoned. There is, however, no evidence of any permanent geographical heterogeneity. The variation within years is thought to be due to the social behaviour of the geese. Family-parties (parents with juveniles) and adults without families tend to form more or less distinct aggregates within any large flock. This point has been explored thoroughly in field studies on white-fronted geese (*Anser albifrons*), in which juveniles are more easily distinguished from adults than in pink-footed geese, but enough observations on the latter have been made to confirm that partial segregation within the flock occurs in this species also. Since the between-catches χ^2 is about ten times too big, the theoretical standard errors quoted for various estimates are about three times too small.

The information provided by the juvenile : adult ratio in the catches is incorporated in the computations to provide estimates of the number of juveniles in 1950, 1952 and 1953 expressed as fractions of the 1950 adult total. There is very little information on the numbers in the different adult age-groups in 1950, since no juvenile : adult ratios for earlier years are available. It is assumed that the number of one- and two-year-olds conformed to their expectations in a population with the (constant) death-rates that are estimated. Finally, the absolute number of adults in 1950 is estimated from the recapture data. The results of these estimations are summarized in Table 4. The death-rates of adults and juveniles are found to be $26 \pm 1{\cdot}6\%$ and $42 \pm 2{\cdot}8\%$ respectively.

Table 4. *Means and standard errors of distributions of possible values of death-rates and reporting-rates, determined from recoveries of ringed pink-footed geese on hypothesis of constant death-rates but varying reporting-rates*

DEATH-RATES (%)

Adults, per annum (year 1 November-31 October): $26 \pm 1{\cdot}6\%$.
Juveniles, from first November to second October of life: $42 \pm 2{\cdot}8\%$.
Goslings, 1951, from marking in July until October, $(1 - \pi)$: $35 \pm 7{\cdot}6\%$.

REPORTING-RATES (Proportion reported of marked birds killed).

1950-51: $\lambda = 34 \pm 4{\cdot}4\%$ 1952-53: $\lambda_2 = 28 \pm 2{\cdot}4\%$
1951-52: $\lambda_1 = 38 \pm 3{\cdot}2\%$ 1953-54: $\lambda_3 = 13 \pm 1{\cdot}8\%$

NUMBERS OF JUVENILES, expressed as % of 1950 adult total.

1950: $83 \pm 6{\cdot}8$ 1952: $29 \pm 2{\cdot}3$
(1951: 44 from death-rates given above) 1953: $50 \pm 3{\cdot}4$

Number of adults in 1950: $28\,000 \pm 3400$.
The standard errors should be treated with reserve (see discussion).

The changes in reporting-rates are of interest because they conform with the trends that might have been expected from the known reaction of wildfowlers to

this study. The publicity given to the Iceland 1951 expedition was sufficient to sustain the interest shown when ringed geese were a novelty, but by 1952 there was some waning of enthusiasm. The sharp drop in 1953 reflects two changes in attitude by fowlers, engendered by the large proportion (15-20%) of geese found to be ringed. To some this caused annoyance, to others loss of interest.

Although the treatment developed above appears to fit the known facts, it is of interest to consider an alternative model wherein it is assumed that there has been no alteration in the proportion of recoveries reported but that the death-rates have varied from year to year. It is highly probable that in fact both death-rates and reporting-rates have varied to some extent, but for the purpose of estimation it is necessary, with the limited information available, to consider one or other factor as approximately constant.

Table 5. *Probabilities of death-rate (d) and survival-rate (e) to be associated with recovery data (Table 6) on the hypothesis that the reporting-rate (λ) remains constant from year to year*

	Date of marking	Probabilities of recoveries				Probabilities of non-recovery so far
		1950-51	1951-52	1952-53	1953-54	
Adults	1950	λd_1	$\lambda e_1 d_2$	$\lambda e_1 e_2 d_3$	$\lambda e_1 e_2 e_3 d_4$	$(1-\lambda d_1-\lambda e_1 d_2-\lambda e_1 e_2 d_3-\lambda e_1 e_2 e_3 d_4)$
	1951		λd_2	$\lambda e_2 d_3$	$\lambda e_2 e_3 d_4$	$(1-\lambda d_2-\lambda e_2 d_3-\lambda e_2 e_3 d_4)$
	1952			λd_3	$\lambda e_3 d_4$	$(1-\lambda d_3-\lambda e_3 d_4)$
Juveniles and goslings	1950 Summer	$\lambda d'_1$	$\lambda e'_1 d_2$	$\lambda e'_1 e_2 d_3$	$\lambda e'_1 e_2 e_3 d_4$	$(1-\lambda d'_1-\lambda e'_1 d_2-\lambda e'_1 e_2 d_3-\lambda e'_1 e_2 e_3 d_4)$
	1951 Autumn		$\pi\lambda d'_2$	$\pi\lambda e'_2 d_3$	$\pi\lambda e'_2 e_3 d_4$	$(1-\pi\lambda d'_2-\pi\lambda e'_2 d_3-\pi\lambda e'_2 e_3 d_4)$
	1951		$\lambda d'_2$	$\lambda e'_2 d_3$	$\lambda e'_2 e_3 d_4$	$(1-\lambda d'_2-\lambda e'_2 d_3-\lambda e'_2 e_3 d_4)$
	1952			$\lambda d'_3$	$\lambda e'_3 d_4$	$(1-\lambda d'_3-\lambda e_3 d'_4)$

Adult death-rates are d_1, d_2, d_3, d_4 successively; d' = juvenile first-year death-rate; $e(=1-d)$ = survival-rate; π = gosling survival-rate, July-Oct. 1951; λ = reporting-rate.

The recovery figures only have been examined using this second model (Table 5), since the inclusion of the juvenile : adult ratios would require several more assumptions about the birth- and death-rates before 1950. This restricts the treatment to the relative magnitude of the death-rates, using a selection of arbitrary values for the proportion of recoveries reported. Standard errors have not been estimated, since their order of magnitude is known from the previous model. The estimates of the annual percentage death-rates using the model of Table 5 are given in Table 6. The goodness of fit of the expected recoveries is very much the same for the two hypotheses and, considering the heterogeneity in the catches, is satisfactory. For the first model $\chi^2=22{\cdot}09$ (11 d.f.), and for the second χ^2 for 9 d.f. is 17·95 ($\lambda=0{\cdot}3$), 18·00 ($\lambda=0{\cdot}4$), or 18·02 ($\lambda=0{\cdot}5$). Although at present it is difficult to decide with confidence whether the first or the second model is more useful, it should not be more than two years before a decision on statistical grounds is possible. When the recoveries from the very large-scale ringing in Iceland in 1953 extend over two or three years, instead of only one, it should be abundantly clear whether the low recovery figures in 1953-54 were due

to an abnormally low death-rate (model 2) or to a drop in the proportion of reported recoveries (model 1).

Table 6. *Estimates of annual percentage death-rates, assuming constant reporting-rate*

Assumed reporting rate-λ (%)	1950-51		1951-52		1952-53		1953-54	1951
	adults	juv.	adults	juv.	adults	juv.	adults	goslings
30	31	38	31	51	26	44	12	32
40	25	30	23	41	18	33	7·5	37
50	21	24	18	33	13	27	5·4	38

(c) *Estimates of the death-rate from recaptures*

Only the British recaptures of British-ringed birds are suitable for the estimation of death-rates, because the Iceland recaptures show clearly that different age-groups differ greatly in liability to capture on the breeding-grounds. The British data are summarized in Table 7. Perhaps the most important feature of this table is the small total of recaptures, in itself sufficient to make it unlikely that estimates of the death-rate derived from them will be at all precise. But considerable interest attaches to the use of recaptures for this estimation because there is no difficulty caused by non-reporting, such as affects the recovery data considered previously.

Table 7. *Recaptures in Britain of British-ringed pink-footed geese*

	Number marked	Number released	Recaptured 1951	1952	1953	1954	Total
Marked as adults	1950	301	5	3	3	6	17
	1951	384	—	6	4	3	13
	1952	897	—	—	21	13	34
	1953	1007	—	—	—	21	21
Marked as juveniles	1950	252	3	4	2	3	12
	1951	141	—	2	6	1	9
	1952	225	—	—	9	2	11
	1953	506	—	—	—	8	8

Leslie & Chitty (1951) have published a critical account of the use of maximum-likelihood equations for estimating the survival factor, $P_1 = 1 - Q$, where Q is the death-rate). Their 'Method A', in which each individual recaptured is counted as many times as it has marks, is used here. The British catches of pinkfeet may be considered as five samplings at yearly intervals. Table 8 records both the solutions for the survival factor for the period 1950-53 and the three separate estimates for three-point samplings which can be obtained from the data. It will be seen that the accuracy of even the long-chain estimate is low, although the value of Q, approximately 21%, is in fairly good agreement with the earlier estimate from recoveries. The estimates from the short chains are included because it is only possible to determine P_1 from a chain of this length; in practice the values of $\tilde{P}_1$ are found to be almost useless, although those for 1951-52 and 1952-53 lead to estimates of Q (45% and 44%) which resemble the 41% found by the use of

recovery data. A second reason for using three-point samplings is because in principle they represent an attractively simple way of determining the annual variations in death-rate, but it is apparent that the accuracy of the estimates must be greatly increased before this can be achieved.

Table 8. *Estimates of the constant annual survival factor (P) for pink-footed geese from British marking and recaptures*

Leslie & Chitty Method A.

Period of estimate	Adults when marked: Survival factor P	Adults when marked: Standard error of P	Adults when marked: Death-rate $Q = 1-P$	Juveniles when marked: Survival factor P_1	Juveniles when marked: Standard error of P_1	Juveniles when marked: Death-rate $Q_1 = 1-P_1$
1950-53	0·793	0·124	*0·207*	no estimate	—	—
1950-51	0·637	0·450	*0·363*	1·0		no estimate
1951-52	0·461	0·251	*0·539*	0·549	0·201	*0·451*
1952-53	0·725	0·256	*0·275*	0·562	0·197	*0·438*

The standard errors should be treated with reserve (see discussion).

(*d*) *Loss of rings*

In the autumn of 1954 there were two instances of recaptures bearing only one ring when they should have had two. (It has been the practice to add a second ring to, or replace the rings on, birds first marked in Britain in 1950 or in Iceland in 1951, while in 1951 and 1952 additional clip rings were put on birds of the year at the time of capture.) The total number of recaptures which carried, or should have carried, two rings was thirty-seven. There has also been one known instance, in twenty possibles, of ring loss amongst white-fronted geese. Both samples are of course very small, but they show that some marks may be lost while the bird remains alive. The indicated proportion of losses, about 5%, is not very serious, but it is clearly important to learn more about such losses and how to prevent them. If it is confirmed that the rate of loss is not negligible it will be necessary to

Table 9. *Monthly distribution of recoveries of pink-footed geese marked as adults or goslings in Iceland in 1951 and 1953 and recovered within one year of marking*

		Month of Recovery: July-mid Sept.	late Sept.-Oct.	Nov.	Dec.	Jan.	Feb.	March-June	Total
	Marked								
Adults	4266	0	26	43	39	38	12	9	167
Goslings	5630	29	113	73	67	67	15	12	376
	9896	29	139	116	106	105	27	21	543
Recoveries per 1000 marked	Adults	0	6·1	10·1	9·1	8·9	2·8	2·1	39·1
	Goslings	5·1	20·0	13·0	11·9	11·9	2·7	2·1	66·7
Monthly totals as % of season total	Adults	0	15·6	25·8	23·4	22·8	7·2	5·4	
	Goslings	7·7	30·0	19·4	17·8	17·8	4·0	3·2	

devise a correction factor. The effect of loss of marks is to underestimate survival. This would affect the use of recovery data as well as of recaptures.

(*e*) *Losses of young geese after arrival in Britain*

The high mortality-rate of geese in the first winter of life has already been established. The comparison of monthly totals of recoveries of goslings and adults (Table 9) suggests that this is due more especially to greater vulnerability in the autumn and early winter. Expressing the number of recoveries as a fraction of the number marked, although emphasizing the difference in recovery-rates between gosling and adults, helps to obscure the difference between the losses suffered by the two classes later in the winter, since as a consequence of heavy early losses the proportion of goslings surviving until January is substantially smaller than the proportion of adults.

Table 10. *First-winter recoveries in Britain of pink-footed geese marked as goslings in Iceland, 1951 and 1953*

Ringed	Oct.	Nov.	Dec.	Jan.	Feb.	March-May	Total
1951	14	24	18	25	8	5	94
1953	99	49	49	42	7	7	253
Totals	113	73	67	67	15	12	347

In Tables 10 and 11 the first-winter recoveries in Britain of goslings ringed in Iceland in 1951 and 1953 are compared with each other and with the monthly percentage recoveries of adults in the same two seasons. The monthly differences in gosling losses resemble those of the adults, except in October 1953. The small

Table 11. *Relative frequencies of monthly recoveries in Britain of Iceland-ringed pink-footed geese in first winter after ringing*

Monthly totals expressed as percentages of season totals.

		Oct.	Nov.	Dec.	Jan.	Feb.-May
1951-ringed	Adults	6·6	15·8	22·4	29·9	28·2
	Goslings	14·9	25·5	19·2	26·6	14·0
1953-ringed	Adults	16·5	25·0	22·6	22·2	13·7
	Goslings	39·2	19·4	19·4	16·6	5·3

number of reported casualties (of both adults and goslings) in October 1951 is of particular interest, because it seems to account for the rather surprisingly low value of the vulnerability quotient V,

$$V = \frac{\text{first-winter recoveries of goslings}}{\text{goslings marked}} \div \frac{\text{first-winter recoveries of adults}}{\text{adults marked}} = 1{\cdot}27$$

obtained from the 1951 sample (Boyd 1953). Since in 1951 the pinkfeet were unusually late in arriving in Britain, the value of V indicated by marking in that year would be abnormally low if juvenile vulnerability is especially great before November. The determination of juvenile mortality by the maximum-likelihood method has shown, however, that despite few recoveries between August and

October 1951 the mortality during this interval was probably high, as in 1953. This discrepancy might be due to reporting failure, but the adult recovery figures make this seem unlikely, since the reporting-rate for 1951-52 was substantially higher than that for 1953-54. If, as it appears, the geese stayed in Iceland in October 1951, the chances of their being reported when shot might have been smaller than in 1953, but this will not constitute a sufficient explanation. The early autumn recoveries of 1953 provide direct evidence that young birds on their first southward migration are relatively unsuccessful in reaching their destination. Of eleven pinkfeet ringed in Iceland in 1953 and recovered in countries not normally visited in considerable numbers by the species (Norway, Sweden, Ireland, the Azores, the Canary Islands) ten were marked as goslings, and nine of eleven recoveries in unusual British localities were also of young birds. Thus the first migration in itself probably causes considerable losses.

Table 12. *Comparative losses of juvenile and adult pink-footed geese from causes other than shooting in first year after marking*

		Ringed	Recovered	Recovery-rate per 1000	Mortality quotient*
Iceland-ringed	Adults	4266	16	3·75	2·79
	Goslings	5630	59	10·48	
British-ringed	Adults	2496	18	7·21	2·11
	Juveniles	1052	16	15·21	

* *R* juvenile/*R* adult.

In this connection it is of some interest to compare the recovery-rates of young and old birds for deaths other than by shooting. This is done for both Iceland- and British-ringed birds in Table 12. In each case the mortality quotient is greater than unity, indicating that young birds are more susceptible to losses than older ones. Although it is likely that some of the casualties included here might have been determined as due to shooting had they been examined or reported on more carefully, it is improbable that such errors in classification would account for this result.

PRODUCTIVITY

(*a*) *Nesting success*

Despite the interest and importance attaching to the breeding-season, the collection of data on nesting success and gosling mortality in an Arctic-nesting species is so difficult that only fragmentary material concerning pinkfoot productivity is available.

There are three sources of information on the numbers of eggs laid by pinkfeet in Iceland. Timmermann (1933) reports clutches of from four to eight, usually five or six, but does not indicate on how many clutches this statement was based. It must, however, refer to nests in the small northern colonies. Congreve & Freme (Freme 1955) found clutches of 4, 5, 6, 6 and 7 in the Krossá colony in 1929. In

1951 (Scott, Fisher & Guðmundsson 1953) the mean of nineteen clutches in the Þjórsárver colony was 4·5, with a range from 3 to 7. According to Salomonsen (1950) clutches in Greenland are usually from 3 to 5, with up to 7 recorded. No detailed records have been published. Salomonsen comments that it is difficult to obtain satisfactory records because nests are subject to predation. The most extensive data on pinkfeet clutches are from Spitzbergen. Koenig & Le Roi (1911) give the measurements of 292 eggs collected or examined here in 1907 and 1908 but, most unfortunately, confine their treatment of clutch-size to the general statements that 4 was normal, 3 or 5 common and from 2 to 9 also occurred, the latter apparently consisting of clutches of 6 and 3 laid by two females in one nest. Examination of Koenig's narrative and of the systematic list by Le Roi appended to his work provides details of sixteen clutches found in 1900 of 2 to 5, mean 3·9. In 1921 the mean of eight clutches found by the Oxford University Expedition was only 2·1, all the clutches being 2 to 4 (Jourdain, unpublished notebooks in Edward Grey Institute). These and other records published by Dalgety, McNeile & Ingram (1931), Mathey-Duprez (1911), Munsterhjelm (1911) and Løvenskiold (1954) lead to a mean of 3·8 for forty-three Spitzbergen clutches, with a range of 1 to 9. It appears possible that the clutch-size in Iceland is larger than in Greenland. The Spitzbergen data also suggest that the mean clutch-size may vary importantly from year to year.

In the Þjórsárver colony egg losses are caused by great black-backed gulls (*Larus marinus*), arctic foxes (*Alopex lagopus*), and arctic skuas (*Stercorarius parasiticus*). Elsewhere in Iceland the collection of eggs by man may formerly have produced serious losses in a few colonies in some years, but has not done so in recent years (Scott & Fisher 1953). Ravens (*Corvus corax*) take many eggs in some of the Iceland colonies. In Spitzbergen and Greenland *L. marinus* is replaced by *L. hyperboreus*. Human predation is probably insignificant in Greenland, where few colonies are visited at all frequently, but may be important in some Spitzbergen colonies. Koenig & Le Roi (1911) mention that in Spitzbergen in 1908 relatively many clutches contained infertile eggs, occasionally several (e.g. 3 of 4, 3 of 5 and 4 of 5). Of twenty-five eggs in eight clutches in 1921 3 of 4 in one nest were addled (Jourdain, unpublished). Members of the 1951 Þjórsárver expedition found only one unhatched egg in 212 but 'noticed rather frequently that one egg had been eaten by predators while the others had survived to hatch' and suggested that the eaten eggs may have been unhatched ones left in the nest.

The only published studies dealing at all extensively with infertility and egg losses in breeding colonies of wild geese refer to the Canada goose (*Branta canadensis*). These show that much variation between and within goose colonies is liable to occur and that any general statements about the magnitude of egg loss for a species with a distribution like that of the pinkfoot must always be uncertain.

(*b*) *Gosling mortality*

The predators taking pinkfoot goslings are those taking eggs, together with the gyr falcon (*Falco rusticolus*), the white-tailed eagle (*Haliaetus albicilla*) and the

snowy owl (*Nyctea scandiaca*). Both the relative and absolute importance of these various predators remain quite unknown. The effects of man are probably more drastic, but more intermittent, than those of the other animals. From the evidence of the 1951 and 1953 Wildfowl Trust expeditions to Þjórsárver and the observations of Taylor & Money-Kyrle (Taylor 1953 and unpublished notes) in the same area in 1952 it seems likely that weather conditions are at least as important as predators in causing gosling losses, but there is very little direct information on this point.

The estimation of gosling losses presents considerable practical difficulties. American workers have used changes in brood-size with age to measure losses before fledging in other species of geese, but it has been shown, notably by Munro (1948) and Miller & Collins (1953), that this method is unsatisfactory because it is common for goslings to attach themselves to broods other than their own at any time during the fledging period. The 1951 Þjórsárver expedition found brood size at hatching to be 4·5 (nineteen broods), the mean of ten broods in the first half of July to be 4·4 and that of eight on 21 July to be 4·2. These data were taken to indicate 'a low mortality rate during the first month'. Lowenskiold (1954) records the sizes of most of the broods seen by him in Spitsbergen in 1948–52. In 1952, the only year for which a usable series is available, the mean of nine broods seen from 7 to 11 July (soon after hatching) was 3·6. By 17 July the mean of eleven was 3·0. Five broods on 14 and 18 August again averaged 3·0. The 1953 Þjórsárver expedition abandoned brood counts. The information obtained by it on gosling losses is derived almost entirely from marked goslings and is discussed by Scott, Boyd & Sladen (1955). Attempts to measure losses from capture-recapture data obtained in Þjórsárver were all unsuccessful, because of incomplete mixing of marked and unmarked goslings, and of goslings found in different parts of the moult. The only method giving acceptable results was based on the comparison of the numbers of recoveries in Britain in winter of goslings ringed early in July with those of goslings not ringed until August. This led to the tentative conclusion that the losses during the fledging period in 1953 may have amounted about three-fifths of the goslings hatched. The same method applied to the 1951 data gives a similar result.

The model for the estimation of first year death-rate (Table 1) included a factor π affecting the expectation of recovery of goslings ringed in Iceland in July 1951 as compared with that of juveniles ringed in Britain in October 1951. The evaluation of this factor led to the conclusion that the losses of goslings between reaching in mid-July and entering the measured British population in mid-October were about 35%. Losses of the same order in 1953 are indicated by three independent methods. Since it appears that losses in late July and early August must be comparatively small, a large part of the estimated losses must occur on the southward migration or immediately after arrival in Britain (mid-September to mid-October).

The methods of estimating losses are all very crude, and direct observations are badly needed, although it will be difficult to achieve them without the observer at the same time contributing importantly to the losses. The Þjórsárver colony

constitutes perhaps nearly as much as a third of the British population so that the rate of loss in this colony has a considerable effect on the numbers of juveniles entering the British population. But it may well be that losses in other smaller colonies in northern Iceland and Greenland differ in incidence and scale from those in Þjórsárver. It seems likely that losses on migration, as well as those sustained soon after hatching may be much affected by weather conditions, so as to vary considerably from year to year.

THE SIZE OF THE BRITISH AUTUMN POPULATION

Two methods are in general use for the determination of the numbers of geese. The first is the direct counting of flocks with the aid of binoculars or from good photographs. Competent observers, in a suitable locality known by them, can achieve consistent results in this way. But skilled observers and suitable conditions are scarce and the necessary conjunction of the two, so that all the pinkfeet in all the areas frequented by them are examined at one time, is most unlikely to be achieved. The Wildfowl Count scheme (Atkinson-Willes 1954) was not intended to achieve 'total counts'. In any event, the principal result from the counts with regard to geese has been to show that the scheme is unsatisfactory for determining goose numbers (although very useful in studying ducks) because counting at fixed localities does not indicate the numbers of geese using an area and because the standard of accuracy achieved by counters is too low.

The results of combining counts made during the autumn rocket-netting expeditions with counts and reports from observers in areas not visited for netting seem to indicate that the British autumn population is not less than 26 000 and not more than 70 000. But an estimate of this kind is subject to many errors and constitutes no more than yet another example of the second common method of determining wildfowl numbers, the use of estimates or general impressions. Since the belief that this approach is unsound is a presupposition of all scientific inquiry, it should be unnecessary to consider it here, but the sad fact is that until very recently there has been no other method available. The consequences have been only too apparent in recent controversies about wildfowl numbers, in which the evidence has consisted almost entirely of general statements asserted by one faction and repudiated, if only for that reason, by others. The development of the rocket-netting technique of catching geese provided another possible means for estimating the numbers of pinkfeet by some of the statistical methods using capture-recapture data. These methods can only give useful estimates if the hypotheses used are appropriate to the sampling practices, so that a description of the latter is a necessary preliminary to the discussion of the methods of estimation.

If marked birds are to be used to provide information about the population as a whole, it is important that the catching and marking of a goose should not affect its liability to capture on a later occasion. This might happen in one of two ways. First, if capture or marking harmed the bird, making it more vulnerable to predators, disease or accidents than unmarked birds, this would lead to a higher mortality rate amongst marked birds. For the British-ringed birds with which we

are here concerned, this is unlikely to be a serious source of error. Capture is known to have increased vulnerability in only six cases, among 460 recoveries from 3800 British-ringed geese. 118 geese were injured or killed by the rocket-nets in 1950-54. Of these the ones unmarked at the time of capture are not included in the totals of birds released and there has only been one British-ringed recapture in the casualties. In most methods of trapping the second factor, the effects of previous capture, is a serious source of difficulty because already-marked birds respond to the trap either by increased reluctance to enter it or by developing a tendency to use the trap as a source of food. It is an important feature of the rocket-net technique that, since the net is concealed, no trap response develops.

The statistical requirement most difficult to meet is that the sampling should be such that any bird has the same probability of being caught as any other and that these probabilities are independent. This represents an ideal impossible to

Table 13. *Numbers of British catches of pink-footed geese and of localities sampled, 1950-54*

Period		Number of catches		Number of localities		Total catch		Length of catching period (days)	
Oct. 1950		14		3		400		20	
Winter 1950-51		21		6		643		?	
Oct. 1951		7		4		520		24	
1952	Oct.	8	16	5	9	580	1133	13	41
	Nov.	8		4		553		13	
1953	Oct.	6	10	4	8	1 063	1558	14	48
	Nov.	4		4		495		12	
1954	Oct.	5	8	4	7	1 145	1572	13	44
	Nov.	3		3		427		8	

achieve in the study of any animal population. In practice all that can be done is to determine whether the occurrences of marked birds in subsequent catches are consistent with the distribution to be expected on the hypothesis of random mixing of marked and unmarked individuals. If this is not so, and no adequate stratified sampling can be devised, the capture-recapture method must be rejected.

The pinkfoot population was evidently of the order of tens of thousands so that it was desirable to secure large samples, of hundreds and preferably of thousands, for the purpose of determining the total numbers with any precision. It remains difficult to catch geese. Single catches of 385 and 345 were made in October 1953, but in earlier years the numbers caught at one time were very much smaller, so that it was necessary to make many catches. Since it was important not to disturb the geese, or even to give grounds for suspicion that this might be happening, the trapping operations had to be spread over as many localities as possible. It was found easiest to catch the geese in stubble-fields, with the results that catching

became restricted to the months of October and November, when incidentally the geese are most numerous and their movements between wintering places are apparently most extensive. Thus the practical requirements of catching led to the concentration of operations into a small part of the year, with as many catches as possible in the period and with these catches spread over several of the major wintering areas of the species. Table 13 shows the result. The localities sampled are spread over six of the seven major areas, but are perhaps better compared with the number of roosts normally occupied by the species, which is apparently about twenty at any one time, though the numbers of geese using these roosts differ very considerably. The short period of trapping enables the whole group of catches in one autumn to be regarded as a unit, giving a series at yearly intervals, and the lumping of catches from scattered localities minimizes the effect of the 'homing' tendency shown by some, but not all, of the flocks sampled, so that the occurrence of recaptures in the whole season is not very much affected by bad sampling. In 1950 and 1951 the sampling was not extensive enough, but it appears that, providing the scale of the operation is large, the sampling is sufficiently nearly random to be acceptable. The numbers of recaptures annually in the years 1951-54 have been so small that no satisfactory statistical investigation of their distribution has been achieved.

(a) *Estimation of total numbers from capture-recapture data*

The simplest form of sample census is that generally referred to as the 'Lincoln index'. If a individuals of a total population x are captured, marked and returned to the population and if on a subsequent occasion r marked individuals are found in a sample of n birds, then the maximum-likelihood estimate of x is given by $\hat{x} = an/r$. The population estimated is that at the time of first marking, not at the second sampling. Bailey (1951, 1952) has shown that this estimate is positively biased and that $\hat{x} = a(n-1)/(r-1)$ provides a better estimate. He demonstrated also that, although an exact value of the variance is not available, V is a nearly unbiased estimate where $V = \frac{a^2(n-1)(n-r)}{(r+1)^2(r+2)}$. But because of the heterogeneity of the catches, in which the within-year variation in the adult : juvenile ratio was ten times greater than the theoretical expectation, and because distribution of recaptures in the years 1951-53 suggests incomplete mixing, this estimate of the variance is certainly too small for the data available here, so that the standard errors given for the estimates of $\hat{x}$ must be regarded as lower limits.

The results of applying Bailey's modification of the Lincoln index method to the British pinkfoot data are shown in Table 14. Some explanation of the grouping of the data is necessary. In 1951 the trapping was confined to October. Subsequently (1952-54) catches were made in two groups, in October and November. In the first season geese were caught in December 1950 and January and March 1951 as well as October 1950, and a second estimate based on the whole season's marking is given, though no precise date can be assigned to it. The limitation to autumn

catching after the first year has already been explained. The splitting of the operation into two is done to avoid the period of the full moon, when the geese feed at night as well as by day, making them more difficult to catch. Mortality from shooting is high during October and November, so that in some years as much as a quarter of the annual losses occurs in these months. Thus this lengthening of the catching period introduces a source of error which could be reduced by making larger catches in a shorter period. It is a necessary condition for the use of the index that no dilution of the population, by births or immigration, occurs in the interval between captures. This fortunately creates no serious difficulty. In autumn pinkfeet born in the preceding summer can readily be distinguished from older birds. Thus n is obtained by subtracting the number of young birds from the

Table 14. *Numbers of pink-footed geese in the British autumn population, 1950-53, estimated by the Lincoln index method*

Date to which estimate refers	Period of first capture	Period of recapture	a	n	r	Autumn population x	Standard error of x
mid-Oct. 1950	Oct. 1950	Oct. 1951	378	384	7	18 200	6000
Winter 1950-51	Oct. 1950-Jan. 1951	Oct. 1951	643	384	8	27 500	8700
mid-Oct. 1951	Oct. 1951	Oct.-Nov. 1952	525	894	8	52 200	16 500
1 Nov. 1952	Oct.-Nov. 1952	Oct.-Nov. 1953	1098	1050	30	37 200	6500
1 Nov. 1953	Oct.-Nov. 1953	Oct.-Nov. 1954	1513	1049	31	49 600	8500

The standard errors should be treated with reserve (see discussion).

total catch, although a, the total of marked birds released, includes birds of the year. Since it appears that the Spitzbergen-breeding pinkfeet enter the British population at a negligible rate the effects of immigration are probably unimportant.

There is another assumption underlying the use of the index, that the death-rate is approximately the same for all age-classes. It has been shown elsewhere that the death-rate of first-winter geese is certainly higher than that of older birds. A correction for this difference is of little value at present because no reliable criteria for identifying second-winter birds have been established, so that no record of the proportion of birds in this class in any sample is available. At the level of accuracy of these estimates the departure from the assumption of a uniform death-rate for all age-classes does not produce serious effects, since the age-distribution in the population is reasonably stable. There are slight indications that the death-rate of older birds may vary with age but even if these differences are confirmed they would have negligible effects on the estimation of total numbers.

(*b*) *Estimation of total numbers from death- and birth-rates*

For the purpose of comparison with the estimates of total numbers obtained by the Lincoln index it is of some interest to construct a table of numbers from the parameters of Table 4. The necessary model and the figures obtained from it are shown in Table 15. This table is at first sight attractively informative, but

closer examination reveals several important weaknesses. First, all the totals are derived from an estimate of the number of adults in 1950, which is not very accurate ($N = 28\,000 \pm 3400$). Thus, should any additional information lead to an increase in the value of N all the subsequent totals would be increased, more or less in proportion. Second, all the components are highly correlated amongst themselves. Third, the calculations require the assumptions that the death-rates of adults and first-year birds remained constant throughout the period and that the juvenile : adult ratio in the catches for the whole period is the average one.

Table 15. *Theoretical age-composition of the British autumn population of the pink-foot, 1950-53 derived from the parameters of Table 4*

d = adult death-rate = 26%; e = survival-rate ($= 1-d$) = 74%; e_1 = first year survival-rate = 58%; N = number of adults in 1950 = 28 000; N_0, N_2, N_3 = number of juveniles in 1950, 1952 and 1953, as % of N.

	Number of birds in October each year					
	Juveniles	16 months	28 months	40 months	Total adults	
1950	N_0	Nd	Nde	Nde^2	N	
1951	$Nd\|e_1$	N_0e_1	Nde	Nde^2	N_0e_1+Ne	
1952	N_2	Nd	N_0e_1e	Nde^2	$Nd+N_0e_1e+Ne^2$	
1953	N_3	N_2e_1	Nde	$N_0e_1e^2$	$N_2e_1+Nde+N_0e_1e^2+Ne^2$	
					Total adults	Total population
1950	23 300	7300	5400	4000	28 000	51 000
1951	12 500	13 500	5400	4000	34 000	46 000
1952	8100	7300	10 000	4000	33 000	41 000
1953	14 000	4700	5400	7400	29 000	43 000

The general picture is of a population which in October consists of between 37 000 and 52 000 geese. The aberrant figure of 18 200 for 1950 is probably more useful as a warning of the dangers of too ready acceptance of such figures than as an estimate of numbers. If only 54·4% (9900) of 18 200 pinkfeet of 16 months or older were alive in October 1950 as this estimate and the juvenile : adult ratio in that year require, an increase to 52 000 a year later would have been impossible. But the 1951 figure itself ($52\,000 \pm 16\,500$) is most unreliable. The virtual uselessness of these estimates for the first two years illustrates the necessity of sampling on as large a scale as possible and over a number of years. Only when several more annual samples of 1500 or more have been obtained will it be possible to make any decisions about the extent of annual fluctuations in numbers.

(*c*) *The number of breeding birds in the population*

For the assessment of the significance of changes in the size of the population it is necessary to know what proportion of the population breeds annually. This will be determined by the age at which sexual maturity is attained, the sex-ratio amongst mature geese, and any factors preventing breeding by mature geese.

The age at which pinkfeet are first capable of breeding is not yet known with certainty. It can only be established by examination of the gonads of a series of geese of known age. Pinkfeet do not breed in the summer following their birth. In 1953 two-year-old geese were distributed within the Þjórsárver colony like older birds, but it is unlikely that any number of them bred (Scott, Boyd & Sladen 1955).

Despite intensive observations on ringed white-fronted geese (*Anser albifrons*), no instances of two-year-olds of that species having reared families have been established (Boyd 1954, and unpublished notes). Recent American studies of *Branta canadensis* have similarly shown that paired two-year-olds occur in breeding colonies but do not breed (Naylor & Hunt 1954, Patterson & Ballou 1953). Geese of various species have bred in captivity at two years, but it will here be assumed that this is not usual in the wild, although alternative calculations including two-year-olds in the breeding population are included.

There were 961 males and 973 females in 1934 adult pinkfeet examined by W. H. Elder and E. A. Maxwell in British rocket-netting catches in 1953 and 1954 (Elder 1955, and unpublished data). For a description of the method of sex determination see Elder (1946). There is as yet no established sex difference in adult death-rate, although the recovery-rate of females is somewhat greater than that of males, and it is unlikely that any difference that may exist would be of sufficient magnitude to invalidate the assumption that for the purpose of a rough calculation of the breeding population the sex-ratio may be regarded as unity.

Table 16. *Estimated numbers of breeding female pinkfeet in Iceland and Greenland, 1951-54, and juveniles surviving to reach Britain in those years, with corresponding brood-sizes at hatching*

Columns A: estimates from data of Table 4 and calculated gosling mortality.
Columns B: estimates from Table 15.

	Number of breeding females				Number of juveniles reaching Britain		Required brood-size at hatching			
	22 months or more		34 months or more				22 months or more		34 months or more	
Year	A	B	A	B	A	B	A	B	A	B
1951	10 400	10 300	—	7600	14 100	12 000	2·7	2·3	—	3·1
1952	14 100	12 700	7700	7800	7400	8200	1·0	1·3	1·9	2·1
1953	11 000	12 200	10 400	9400	16 100	14 000	2·9	2·2	3·4	2·9
1954	12 400	—	8200	—	14 100	—	1·1	—	1·7	—

Estimates of the numbers of sexually mature females in the summers of 1951 to 1954 are recorded in Table 16, on the alternative assumptions that all geese 22 months old are mature and that maturity is not reached until a year later. The totals have been computed, first, by calculating the survivors in the years $n-1$ or $n-2$ of the 'adults' alive in the autumn of year n, applying the adult survival factor 0·74 to the best estimates of population size (column A), and second from the estimates of the size of age-classes shown in Table 15 (column B). It is assumed that adult mortality in summer is negligible, since only 1·2% of recoveries have been obtained from May to September.

It may be recalled that the limited data on mean brood-size at hatching ranged from 2·6 in Spitzbergen in 1952 to 4·5 in Iceland in 1951. Since the lower of these figures is appreciably greater than the maximum brood-size required from females of 32 months or more (3·4 in 1953) and much greater than that required if 20-month-old females also breed, the calculations summarized in Table 16 indicate either that second-summer females do not breed or that if they do a very large

proportion of birds of breeding age fail to hatch any young. If the first alternative is accepted, we still find a range of 1·7-3·4 in the required brood-size and a 1951 value of 3·1 as compared with the observed 4·5. This suggests that perhaps only about 70% of the mature females hatched any young in 1951, a year in which the weather in May and June was favourable for breeding. 1952 was a very bad year for the breeding of all species of birds in Iceland (Taylor 1953, Money-Kyrle & Taylor, unpublished report), the spring being unusually warm, leading to early egg-laying, but with heavy snowstorms at the end of May and unusually cold and wet weather for most of June, which led to the wholesale abandonment of nests during the incubation period and to serious losses of young birds. Thus it may well be that the implication of the 1952 entries in Table 16, that perhaps half the mature females failed to hatch any young, is in accord with the facts. The indication that 1953 was a good year and 1954 rather a bad one for breeding also conform with expectations from the meteorological evidence. The suggestion that even in climatically favourable years like 1951 and 1953 at least a quarter of the mature females hatched no young, emphasizes the need for further studies of the pinkfoot in the nesting season.

ACKNOWLEDGMENTS

This study was initiated by Mr Peter Scott, Hon. Director of the Wildfowl Trust, to whom the success of the goose-catching expeditions on which it is based has been very largely due. I am much indebted to Mr Scott for his continued encouragement. Mr Neil Gilbert of the Department of Genetics, University of Cambridge, devised the methods of estimating adult death-rates from recoveries, performed the calculations in that part of the paper and criticized an earlier draft. Mr P. H. Leslie, Dr D. Chitty and Mr H. N. Southern of the Bureau of Animal Population, University of Oxford, gave valuable advice in the early stages of the investigation. Dr D. J. Finney, Marischal College, Aberdeen, very kindly criticized a draft of this paper. To all these, and to over 700 others who have assisted the study, as members of goose-catching expeditions, by reporting recoveries, or in other ways, I am very grateful.

SUMMARY

1. This account of the British-wintering population of the pink-footed goose *Anser brachyrhynchus* is based on the marking of over 14 800 geese captured in Britain and Iceland since 1950-54. This population, breeding in Greenland and Iceland, is almost independent of the one breeding in Spitzbergen and wintering in Germany, Denmark and Holland.

2. Of 982 reported casualties, 89% were due to human activities, nearly all in Britain; other causes of adult losses are probably of minor importance.

3. Estimates of adult death-rates from recoveries of marked birds are made by the use of two models. In the first, the annual death-rate is supposed constant but the reporting-rate is allowed to vary. In the second, the reporting-rate is assumed constant at some arbitrary value, and the death-rate is variable. The

first model seems to fit the data better. On this model the death-rate of geese more than one year old in a year 1 November to 31 October, is $26 \pm 1{\cdot}6\%$, while the death-rate of geese between 4 and 16 months old is $42 \pm 2{\cdot}8\%$. Using the second model adult death-rates range from 5·4% (with reporting-rate 50%) to 31% (reporting-rate 30%).

4. Estimates of death-rates from capture-recapture data are $21 \pm 12\%$ per annum for geese more than a year old, and $44 \pm 20\%$ in the interval 4-16 months.

5. In 1951 and 1953 losses of goslings in the largest known colony were of the order of 60% between hatching and arrival in Britain.

6. The size of the British population was estimated by a capture-recapture method to have been $37\,200 \pm 6500$ on 1 November 1952 and $49\,600 \pm 8500$ on 1 November 1953. A method of estimating total numbers (at 1 November) from the calculated death-rates leads to values of from 41 000 to 51 000 in the years 1950-53.

7. The sex-ratio is very nearly 1 : 1. Most individuals probably do not breed until 32 months old. The numbers of sexually mature females in 1951-54 are estimated at 7600-10 400.

8. The observed mean clutch size is 4·5; this may be subject to seasonal and regional variations, but is substantially higher than the size required for replacing estimated losses. It is concluded that the complete nesting failure of a substantial part of the potential breeding population is usual, even in climatically favourable years.

REFERENCES

Atkinson-Willes, G. (1954). *National Wildfowl Counts, 1925-1954.* London.

Bailey, N. T. J. (1951). On estimating the size of mobile populations from recapture data. *Biometrika,* **38,** 293-306.

Bailey, N. T. J. (1952). Improvements in the interpretation of recapture data. *J. Anim. Ecol.* **21,** 120-7.

Boyd, H. (1953). Notes on the relative mortality of adult and young Pink-footed Geese. *Rep. Severn Wildf. Tr.* **5,** 28.

Boyd, H. (1954). White-fronted Goose statistics, 1952-53. *Rep. Wildf. Tr.* **6,** 73-9.

Dalgety, C. T., McNeile, J. H. & Ingram, M. J. (1931). Notes on birds observed in Spitzbergen during the spring of 1930. *Ibis* (12) **7,** 243-55.

Elder, W. H. (1946). Age and sex criteria and weights of Canada Geese. *J. Wildlife Mgmt.* **10,** 93-111.

Elder, W. H. (1955). The relation of age and sex to the weights of Pink-footed and Greylag Geese. *Rep. Wildf. Tr.* **7,** 127-32.

Fisher, R. A. (1954). *Statistical Methods for Research Workers.* 12th ed. Edinburgh.

Freme, S. W. P. (1955). The discovery of Pink-footed Geese nesting in Iceland, 1929. *Rep. Wildf. Tr.* **7,** 139-45.

Goodhart, J., Webbe, R. & Wright, G. T. (1955). Goose-ringing in West-Spitzbergen 1954. *Rep. Wildf. Tr.* **7,** 170-6.

Hickey, J. J. (1952). Survival studies of banded birds. *Spec. Sci. Rep. U.S. Fish Wildl. Serv.* No. 15, 1-177.

Koenig, A. & Le Roi, G. (1911). *Avifauna Spitzbergensis.* Bonn.

Leslie, P. H. & Chitty, D. (1951). The estimation of population parameters from data obtained by means of the capture-recapture method. I. The maximum-likelihood equation for estimating the death-rate. *Biometrika,* **38,** 269-92.

Løvenskiold, H. L. (1954). Studies on the avifauna of Spitzbergen. *Skr. Norsk Polarinst.* No. 103, 1-131.

Mathey-Duprez, A. (1911). Notes ornithologiques recueillies au cours des croisières de l' 'île de France' en Norvege et en Spitzberg. *Bull. Soc. neuchâtel Sci. nat.,* 1910, 39-55.

Miller, A. W. & Collins, B. D. (1953). A nesting study of Canada geese on Tule Lake and Lower Klamath National Wildfowl Refuges, Siskiyou County, California. *Calif. Fish Game,* **39,** 385-96.

Munro, J. A. (1948). Waterfowl breeding conditions in British Columbia, 1948. *Spec. Sci. Rep. U.S. Fish Wildl. Serv.* No. 60, 13-25.

Munsterhjelm, L. (1911). Beobachtungen während einer ornithologischen Studienreise nach den Nordpolarmeer und Spitzbergen in Sommer 1910. *Äfvers. finska Vetensk Soc. Förh.,* **53** (20), 1-42.

Naylor, A. E. & Hunt, E. G. (1954). A nesting study and population survey of Canada Geese on the Susan River, Lassen County, California. *Calif. Fish Game,* **40,** 5-16.

Patterson, R. L. & Ballou, R. M. (1953). The status of the Canada Goose in Wyoming. *Wyoming Wild Life,* **17,** 4-14.

Salomonsen, F. (1950). *Birds of Greenland.* Copenhagen.

Scott, P., Boyd, H. & Sladen, W. J. L. (1955). The Wildfowl Trust's second expedition to Central Iceland, 1953. *Rep. Severn Wildf. Tr.* **7,** 63-98.

Scott, P. & Fisher, J. (1953). *A Thousand Geese.* London.

Scott, P., Fisher, J. & Gudmundsson, F. (1953). The Severn Wildfowl Trust expedition to Central Iceland, 1951. *Rep. Severn Wildf. Tr.* **5,** 78-115.

Taylor, J. (1953). A possible moult-migration of Pink-footed Geese. *Ibis,* **95,** 638-42.

Timmermann, G. (1933). Die Kurzschnabelgans in Island. *J. Orn. Lpz.* **81,** 322-30.

THE ARTHROPODA OF THE SOIL IN A WEST AFRICAN PASTURE

By W. BELFIELD

University College of the Gold Coast, Achimota

(With 4 Figures in the Text)

Much work has been done on the micro-fauna of the soil in various parts of the world. The main proportion of this, however, has been carried out in Europe and America. A certain amount has also been carried out in and around the West Indies (Dammerman 1925, 1937, Strickland 1945, 1947). Only one piece of research has been done in tropical Africa, and that in East Africa (Salt 1952).

Apart from the more obvious soil fauna such as termites, ants and other micro-fauna living in the soil which have been observed by collectors, no observations on West African soil arthropods have been made. Nothing is known of the vertical, horizontal or seasonal distribution and variation of the smaller forms. Work has, therefore, been started in an attempt to gather some information about one particular area in the Gold Coast, the Accra plains.

This paper contains the results of the first part of this work. It is an attempt to find the vertical distribution of the various groups of the arthropods in pasture soil throughout the dry and wet season, i.e. from December 1953 to May 1954.

METHODS

As it was intended to take monthly samples on a comparative basis, and the water and electrical supply could not be relied upon to be good at any particular time, it was necessary that any apparatus used for extracting the animals from the soil should not require a good supply of either of these services. It was, therefore, decided to use Ladell's method of extraction (Ladell 1936). This is a flotation device using a 25% solution of magnesium sulphate, which gives a specific gravity of 1·11. This solution floats the arthropods out of the soil, which is being stirred thoroughly. Air is bubbled through the soil at the same time to ensure that it is completely broken up. If necessary, this apparatus can be worked manually, and the air supply delivered from a car tyre pump.

Although Ladell's method has been shown to be less efficient than some other methods (Macfadyen 1953), it has the advantage, as shown above, that it does not require water at high pressure as would be necessary in Salt & Hollick's method, nor does it require a steady electrical supply as would be necessary in the use of funnel methods. Macfadyen had not published an account of his paraffin-burning development of the Tullgren-type funnel when this work was first started.

Because of the necessity of separating the animals from the vegetable matter coming from the apparatus a modification of Ladell's original method similar to

the one used by Glasgow was introduced (Glasgow 1939). The resulting animals floated out from the apparatus were filtered off in a Buchner funnel. The filter paper with its contents were then transferred to a petri dish, more magnesium sulphate added, and examined by means of a binocular microscope. The use of a microscope mechanical stage modified to fit a petri dish, ensured that the whole of the dish was examined.

The samples of soil were removed by means of a soil corer (K.C. Productions Ltd, Model 110) of 4 in. diameter and 18 in. deep. This instrument has many advantages for use in the soils of the Accra plains, which are to a large extent gravelly.

These advantages include a removable cutting head, and a very heavy jarring link, which was especially useful as it enabled the sampling tube to be driven in despite the iron concretions. The sampling tube was removed from the soil by means of a lorry-raising jack in order that the removal could be accomplished neatly and with as little disturbance of the surrounding soil as possible. The soil samples were removed from the tube by means of a piston arrangement worked by a hydraulic jack.

The cores, which were 18 in. long, were cut into sections, these sections being, the top 2 in., 2-4 in., 6-12 in. and 12-18 in. The top 6 in. was split into 2 and 4 in. in order to ascertain the proportions of animals at or near the surface in the top 6 in. By adding these two top samples of 2 and 4 in. together the results could be compared with those of many other workers who have taken the top 6 in. without any division. Samples were taken to a depth of 18 in., because it was felt that the lower levels of the soil would assume importance during the dry season. It is admitted that there will be a loss of animals because of this handling. Each sample, however, was treated in exactly the same way, therefore the results will be comparable.

Lack of records and the traditional shifting method of agriculture used by African farmers made the finding of an area which could be regarded as unspoiled pasture land difficult. An area of about fifteen acres situated in the Agricultural Station, Pokoase, was eventually chosen. This field had been used intermittently for grazing over the past ten years. Six stations were established in this field and a sample taken from each station every month, in such a way that each was within a yard of at least two other samples at the station. By this method of sampling, the vertical distribution of the soil fauna throughout the period could be determined.

Table 1. *Monthly rainfall and temperature at Pokoase*

	Dec.	Jan.	Feb.	Mar.	Apr.	May
Total rainfall (in.)	0·01	0·80	4·77	3·65	5·51	7·31
Number of rain days	1	4	3	6	11	12
Mean temperature at 1500 h (°F)	88·3	87·5	87·1	86·9	84·3	83·8

The period of examination chosen was from December 1953 to May 1954. The rainfall figures for this period may be found in Table 1. It can be seen from these figures that December and January are very dry, and February, March, April and May are progressively wetter.

RESULTS

Table 2 gives the total number of animals removed from all six samples during the observation period at the various depths. The totals of the samples from all six stations were used in order to give a clearer idea of the overall distribution. Table 3 shows that these totals can be used as a representation of the distribution of the soil fauna and gives the monthly totals of each station expressed as a percentage of the monthly total for all the stations; it can be seen that except for the March figure at Station B this percentage does not vary a great deal in the period of sampling. It may be seen that the highest standard deviation is 7% at Station B. Table 3 also gives similar figures calculated for the main groups of animals found. Here again the standard deviation is low. It is felt that this shows that there is no marked deviation from the general pattern at any of the stations and, therefore, the totals from all the stations can be compared on a monthly basis. Isoptera and Formicidae are not included in the monthly totals of Table 2, as they were considered to be aggregated animals. Samples were taken as far away as possible from the nests of these two orders. If, however, these animals were found in any quantity in a sample, it was rejected and another taken. The main reasons for this rejection are that the available volume of soil for other animals would be very much reduced by their tunnels, there is often a quite specialized fauna living in the nests, and the effect of the activities of these animals on the surrounding microhabitats is not certain.

Table 2. *Total numbers, and total numbers of various groups found*

	Top 2 in.	2-6 in.	0-6 in.	3×2 in.	3/2×2-6 in.	6-12 in.	12-18 in.	Total
TOTAL NUMBERS								
December	56	66	122	168	99	156	68	346
January	73	88	161	219	132	169	144	474
February	152	202	354	456	303	213	101	668
March	250	260	510	750	390	235	131	876
April	305	271	576	915	406	258	91	925
May	431	316	747	1293	474	203	95	1045
Total	1267	1203	2470	3801	1804	1234	630	4334
DIPLURA								
December	0	1	1	0	2	2	0	3
January	0	2	2	0	3	3	3	8
February	4	3	7	12	5	2	2	11
March	3	3	6	9	5	1	9	16
April	1	6	7	3	9	8	4	19
May	1	2	3	3	3	3	6	12
Total	9	17	26	27	27	19	24	69
COLLEMBOLA								
December	3	27	30	9	41	44	13	87
January	5	16	21	15	24	43	27	91
February	39	60	99	117	90	38	12	149
March	51	75	126	153	113	42	29	197
April	124	88	212	372	132	81	21	314
May	175	95	270	525	143	41	15	326
Total	397	361	758	1191	543	289	117	1164

	Top 2 in.	2-6 in.	0-6 in.	3 × 2 in.	3/2 × 2-6 in.	6-12 in.	12-18 in.	Total
[illegible] PSOCOPTERA								
December	11	3	14	33	5	5	0	19
January	6	3	9	18	5	0	3	12
February	14	12	26	42	18	1	1	28
March	11	2	13	33	3	2	1	16
April	3	0	3	9	0	2	0	5
May	1	0	1	3	0	0	0	1
Total	46	20	66	138	31	10	5	81
[illegible] NOPTERA								
December	0	0	0	0	0	0	1	1
January	0	0	0	0	0	1	1	2
February	0	0	0	0	0	0	0	0
March	0	0	0	0	0	0	0	0
April	1	0	1	3	0	1	0	2
May	0	0	0	0	0	0	0	0
Total	1	0	1	3	0	2	2	5
[illegible] PTERA								
December	0	0	0	0	0	0	0	0
January	2	0	2	6	0	0	0	2
February	3	5	8	9	8	8	0	16
March	0	3	3	0	5	13	0	16
April	3	19	22	9	29	2	4	28
May	1	1	2	3	2	5	1	8
Total	9	28	37	27	44	28	5	70
[illegible] LEOPTERA								
December	0	1	1	0	2	0	0	1
January	2	0	2	6	0	2	4	8
February	0	0	0	0	0	0	0	0
March	0	0	0	0	0	1	0	1
April	0	0	0	0	0	0	0	0
May	0	0	0	0	0	0	0	0
Total	2	1	3	6	2	3	4	10
[illegible] MORUDAE								
December	1	0	1	3	0	2	2	5
January	3	0	3	9	0	5	0	8
February	1	3	4	3	5	2	1	7
March	4	2	6	12	3	2	2	10
April	1	5	6	3	8	1	2	9
May	2	1	3	6	2	0	3	6
Total	12	11	23	36	18	12	10	45
[illegible] PTERA								
December	1	1	2	3	2	0	0	2
January	2	2	4	6	3	0	3	7
February	3	1	4	9	2	1	1	6
March	1	1	2	3	2	0	0	2
April	3	0	3	9	0	0	2	5
May	0	1	1	0	2	0	3	4
Total	10	6	16	30	11	1	9	26
[illegible] CHELOGNETHI								
December	0	2	2	0	3	5	1	8
January	0	1	1	0	2	5	1	7
February	5	2	7	15	3	6	2	15
March	0	3	3	0	5	17	9	29
April	0	1	1	0	2	8	3	12
May	0	2	2	0	3	13	2	17
Total	5	11	16	15	18	54	18	88
[illegible] PALPIGRADI								
December	0	0	0	0	0	0	1	1
January	0	0	0	0	0	0	1	1
February	0	0	0	0	0	2	3	5

	Top 2 in.	2-6 in.	0-6 in.	3×2 in.	3/2×2-6 in.	6-12 in.	12-18 in.	Total
March	0	0	0	0	0	3	9	12
April	0	0	0	0	0	2	15	17
May	0	0	0	0	0	4	8	12
Total	0	0	0	0	0	11	37	48
ACARINA								
December	39	27	66	117	41	63	29	158
January	49	53	102	147	80	52	44	198
February	76	80	156	228	120	89	38	283
March	150	140	290	450	210	90	49	429
April	146	98	244	438	147	79	25	348
May	233	135	368	699	203	85	38	491
Total	693	533	1226	2079	801	458	223	1907
CHILOPODA								
December	1	1	2	3	2	0	3	5
January	0	1	1	0	2	0	0	1
February	0	0	0	0	0	0	0	0
March	1	1	2	3	2	0	0	2
April	0	0	0	0	0	2	1	3
May	0	1	1	0	2	1	1	3
Total	2	4	6	6	8	3	5	14
DIPLOPODA								
December	0	0	0	0	0	0	0	0
January	0	0	0	0	0	0	1	1
February	0	1	1	0	2	1	0	2
March	0	0	0	0	0	0	0	0
April	0	0	0	0	0	1	0	1
May	0	2	2	0	3	2	0	4
Total	0	3	3	0	5	4	1	8
PAUROPODA								
December	0	0	0	0	0	11	6	17
January	4	4	8	12	6	22	22	52
February	3	7	10	9	11	14	13	37
March	14	11	25	42	17	16	7	48
April	16	18	34	48	27	23	8	65
May	14	30	44	42	45	15	11	70
Total	51	70	121	153	106	101	67	289
SYMPHYLA								
December	0	3	3	0	5	24	12	39
January	0	6	6	0	9	36	34	76
February	4	28	32	12	42	49	28	109
March	15	19	34	45	29	48	16	98
April	7	36	43	21	54	47	6	96
May	4	46	50	12	69	33	5	88
Total	30	138	168	90	208	237	101	506

Columns 3, 4 and 5 of Table 2 are adjustments of the figures obtained from the top 6 in. Column 3 is obtained by adding the top 2 in. and the 2-6 in. figures together giving, therefore, the total animals in the top 6 in. Column 4 is obtained by multiplying the top 2 in. figures by three, thus making them comparable to the animals extracted from 6 in. of core. Column 5 is obtained by multiplying the 2-6 in. figures by 1·5, which again makes the figures comparable to the figures obtained from 6 in. of the core.

The most striking results obtained from these figures is the continual rise of the total number of animals from December to May. This corresponds to the increased rainfall (Fig. 1). Some measure of this increase may be realized when it is seen that the total numbers in May are more than treble the numbers in December.

Table 3. *Numbers at each station expressed as percentages of the monthly totals for all stations*

	Stations					
	A	B	C	D	E	F
December	21	8	9	13	29	21
January	19	12	15	11	27	17
February	17	15	16	18	22	19
March	20	29	10	16	20	22
April	21	16	15	17	21	11
May	14	11	13	23	26	13
Total	112	91	78	98	145	103
Arithmetic Mean	19	15	13	16	24	17
Standard Deviation	2·5	6·7	2·6	3·6	3·3	4·0
COLLEMBOLA						
December	39	10	10	15	17	8
January	20	11	11	12	31	18
February	13	10	7	31	16	23
March	25	11	16	21	22	6
April	7	6	12	37	19	18
May	17	11	12	25	20	15
Total	121	59	68	141	125	88
Arithmetic Mean	20	10	11	23	21	15
Standard Deviation	10·1	1·8	2·7	8·6	5	5·9
ACARINA						
December	6	5	6	11	42	30
January	19	15	12	10	31	14
February	15	15	17	28	29	14
March	26	12	9	12	17	24
April	20	21	17	12	18	11
May	11	13	14	17	31	14
Total	97	81	65	90	168	107
Arithmetic Mean	16	13	11	15	28	18
Standard Deviation	6·5	4·8	4·4	6·2	11·6	6·7
PAUROPODA						
December	59	23	6	0	0	11
January	52	4	12	2	25	6
February	46	27	14	11	3	0
March	15	17	23	6	21	19
April	46	15	18	9	6	5
May	41	26	16	7	4	6
Total	259	112	89	35	59	47
Arithmetic Mean	43	19	15	6	10	8
Standard Deviation	13·7	8	5·3	3·8	9·4	5·9
SYMPHYLA						
December	5	8	10	33	20	23
January	9	4	16	20	14	39
February	5	2	0	38	24	31
March	3	0	2	39	46	10
April	5	5	1	29	32	27
May	25	2	5	25	41	23
Total	52	21	34	184	177	153
Arithmetic Mean	7	4	6	31	30	26
Standard Deviation	7·7	2·6	4·6	6·8	9·6	8·8

Using only figures for the three sections of the core 0-6 in., 6-12 in. and 12-18 in. (Table 2), it may be seen that the greatest density of animals in December was between 6 and 12 in. In January the maximum, though not so marked, was still at the same depth. From February to May the maximum density was markedly in the top 6 in. In fact the difference between the numbers found in the top 6 in.

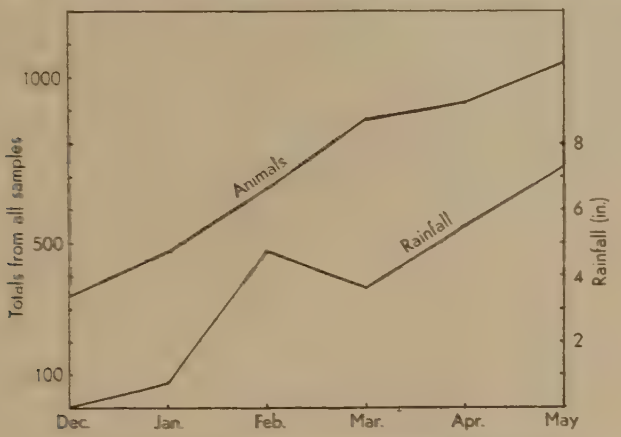


Fig. 1. Total animals collected in each month, and rainfall.

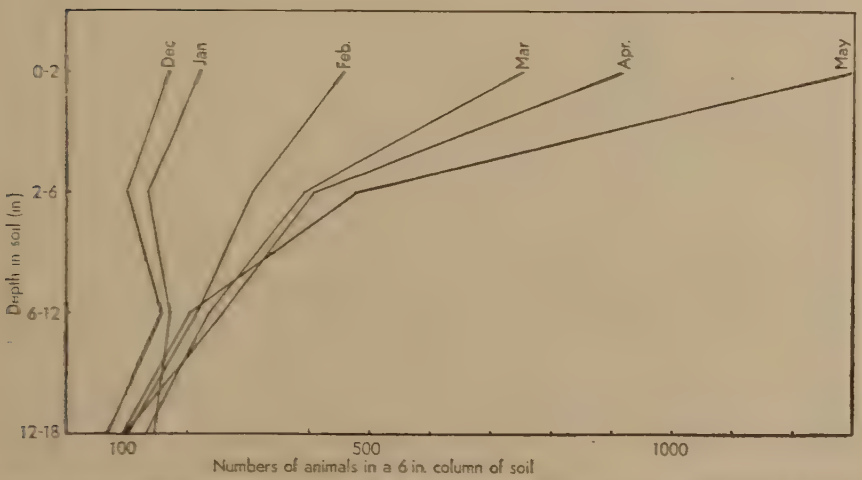


Fig. 2. Total animals collected each month at different depths. The figures for the top 2 in. and 2-6 in. are corrected to correspond to 6 in., i.e. columns 4 and 5 in Table 2a.

and the rest of the sample became greater from February to May. The lowest section was the lowest density throughout the period of observation. It can be seen from this that the majority of the soil animals are below 6 in. during the dry season and in the top 6 in. during the wet season.

Fig. 2 is a representation of the figures from columns 4, 5, 6 and 7. It may be seen from this that when the numbers for the top 2 in. are adjusted to compare with 6 in. of the core, the greatest density of animals is seen to be in the top 2 in. throughout the observation period. This density increases as the season becomes wetter. The density of the animals in the 2-6 in. section also increased during the same period, but this increase is not so great as that in the top 2 in. The numbers found in the bottom 6 in. were roughly similar throughout the six months. It can, therefore, be stated that the greatest density of animals was always in the top 2 in. and that this density increases as the season becomes wetter.

The results obtained from the individual orders extracted from the soil are found in the rest of Table 2, and will be discussed separately.

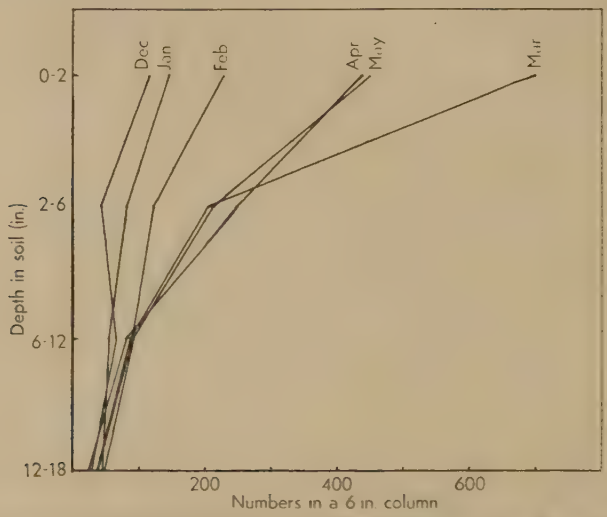


Fig. 3. Total Collembola collected in each month at different depths. The figures for the top 2 in. and 2-6 in. are corrected to correspond to 6 in., i.e. columns 4 and 5 in Table 2.

Diplura. It may be seen that there is a general increase in numbers throughout the period. They seem to show no marked preference for any particular depth, and the totals and corrected totals for the various depths show a remarkable similarity.

Collembola. There is a marked increase in numbers of this order throughout the period. Their vertical distribution changes as the season becomes wetter. The lowest density was in the lowest section of the core all the time. The highest density in December and January is in the sections 2-6 in. and 6-12 in. From February onward, however, the highest density is in the top 6 in. This is mainly due to the great increase in density in the top 2 in. Fig. 3 illustrates this increase in density in the top 2 in. The difference in numbers in the top 2 in. from January to February is quite marked, being nearly eight times as many. It seems certain, therefore, that this order is very much affected by the water content of the soil. (See Table 1).

Corrodentia. The numbers are rather low in this order. It does seem, however, that they show a preference for the upper layers of the soil, especially the top 2 in. There seems also to be a drop in numbers in April and May, contrary to the general trend of the rest of the fauna.

Hemiptera. Because of the small numbers captured, little can be said about this order, except that they were very few in number in January and February. Also few are to be found below 12 in. This could be because of association with grass roots.

Hymenoptera. The Hymenoptera found were of the two families Mymaridae and Formicidae. The Formicidae were disregarded for the reasons stated above. Mymaridae, although not common did appear in every sampling, with apparently little variation in numbers throughout the period. The numbers captured are too low to show conclusively any vertical distribution. It does seem possible, however, that they are more prevalent in the top 2 in.

Chelonethi. There is no gradual increase in numbers throughout the period although the numbers for December and January are the lowest. The vertical distribution, however, is quite definite. Except in February none were found in the top 2 in. They were found between 2 and 6 in. in every sampling but not in any quantity, in fact there were slightly more between 12 and 18 in. than between 0 and 6 in. The maximum density is quite obviously in the 6-12 in. section. Three times as many Chelonethi were found in the 6-12 in. section as in the 0-6 in. or 12-18 in. sections.

Palpigradi. There is an increase in numbers during the period, only one animal being found in December and January. There is, however, despite the low numbers found, a very clear vertical distribution. None were found in the top 6 in. at all, but most were found between 12 and 18 in., where there were more than three times as many as between 6 and 12 in.; even 18 in. may not be their level of maximum density.

Acarina. There is a definite increase in numbers as the year progresses. As in the case of the Collembola, the density shows a great increase in the top layers as the period progresses (Fig. 4). There is only one exception to this, December, when the density of the 2-6 in. layer is slightly lower than the 6-12 in. density.

Pauropoda. The increase in total numbers is not very definite but there does seem to be one. The maximum vertical distribution varies. In December, January and February the maximum density is between 6 and 18 in. The maximum in February though, is not so definite. In March, however, there is a large increase in numbers in the top 2 in. and to a lesser extent between 2 and 6 in. In March and April the maximum density is in the top 2 in., but in May is in the top 6 in. The densities of the other sections become less as lower levels are attained.

Symphyla. The seasonal distribution of this order is not perfectly clear. The totals for December and January are the lowest, but then February is the highest total, and March, April and May totals gradually become less. Vertical distribution is

also rather complex. The maximum density in December is between 6 and 12 in. In January the densities of the 6-12 in. and 12-18 in. sections are almost equal and are both much greater than the two upper sections. In February the densities of the 2-6 in. and 6-12 in. sections are almost equal and are each greater than the top 2 in. section and the bottom 6 in. In March the densities of the 6-12 in. and the top 2 in. are almost equal and are each greater than the other two sections. In April and May the greatest density is in the 2-6 in. section. There is a drop in the density of the top 2 in. and bottom 6 in., though the 6-12 in. section still remained

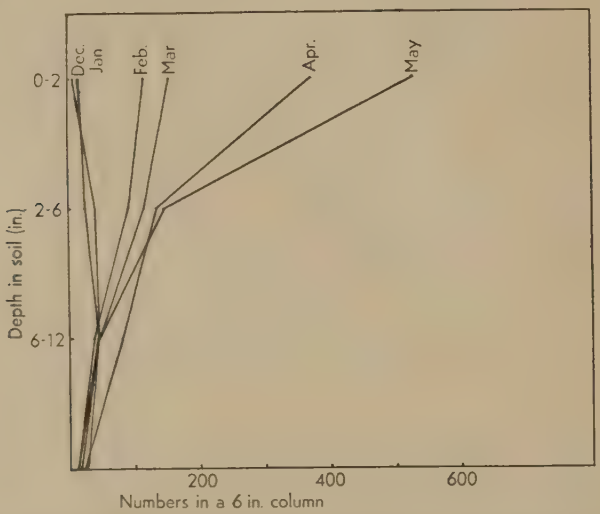


Fig. 4. Total Acarina collected in each month at different depths. The figures for the top 2 in. and 2-6 in. are corrected to correspond to 6 in., i.e. columns 4 and 5 of Table 2.

quite high. It seems, therefore, that as the year progressed the maximum density moved from the bottom two sections to the 2-6 in. section except for the odd result in March when the maximum was in the top 2 in. There was also a reduction in numbers found in the bottom section as the year progressed. The total number of Symphyla found throughout the period, however, was greatest in the 6-12 in. sections. The shift of maximum density is, therefore, upwards as in the case of the Collembola and Acarina. The Symphyla, however, do not occupy the top 2 in. to the same extent as these other two groups.

Because of the small numbers captured, little can be concluded about the Protura (1), Thysanoptera (5), Coleoptera (10), Diptera (26), Araneida (2), Phalangidae (1), Chilopoda (14), or Diplopoda (8).

Table 4 shows the percentage of the total, of each group of arthropods. Similar figures are included from East Africa, and a pasture in England (Salt 1952), for comparison. It may be seen from the first three columns of this table that in all the areas, the Acarina and Collembola account for a very high proportion of the population, i.e. England 88%, East Africa 86% and West Africa 80%. There is,

however, a difference in the proportions of the two groups. The figures for Collembola are similar in England and here in West Africa, but lower in East Africa, but in the case of the Acarina the figures for England and East Africa are similar, and lower in West Africa.

The main differences to be noted from this table are that the Pauropoda and Symphyla are obviously higher here than in either England or East Africa. Other differences are a higher proportion of Psocoptera here than in the other two areas, and lower proportions here in the cases of the Thysanoptera, Hemiptera and Coleoptera.

Table 4. *Percentage of various groups in total population of pasture soils*

	Cambridge Top 6 in.	E. African Top 6 in.	W. African Top 6 in.	W. African 6-18 in.
Thysanura	2·3	0·2	1·0	2·3
Collembola	28·3	17·0	30·6	22·0
Psocoptera	0·04	0·3	2·7	0·8
Thysanoptera	0·9	1·1	0·04	0·2
Hemiptera	2·9	11·3	1·5	1·8
Coleoptera	3·0	4·6	0·1	0·4
Lepidoptera	0·07	0·5	—	—
Diptera	0·7	1·2	—	—
Hymenoptera	1·8*	—	0·9†	1·2†
Acarina	60·0	69·9	49·5	36·5
Araneida	0·2	0·3	—	—
Chelonethi	0·01	0·5	0·6	3·9
Palpigradi	—	0·2	—	2·6
Chilopoda	0·2	0·3	0·2	0·4
Diplopoda	0·2	0·3	0·1	0·3
Pauropoda	—	0·4	4·9	9·0
Symphyla	0·8	2·2	6·8	18·1

* Formicidae. † Mymaridae.

Within the West African samples there is a marked difference between the fauna of the top 6 in. and that of the lower samples. The Collembola and Acarina are very much fewer, the Symphyla, Pauropoda, Palpigradi and Chelonethi, very much more numerous. The reason for this is to be found in the vertical distribution of these groups. It is interesting to note that the Thysanura and Psocoptera show similar proportions at this lower depth to the proportions found in the top 6 in. in England and East Africa. This seems to indicate that the distribution of these groups is at a lower level here than in the other areas. On the whole, however, this table shows a remarkable similarity in the proportions of the groups to the total fauna in these three widely separated areas.

DISCUSSION

This method of sampling appears to be successful in showing the vertical distribution of the soil fauna over a period of time. It has shown many points of value.

The increase in numbers as the wet season progresses could be expected from the appearance of the soil. In December and January the top few inches of soil is hard-baked and completely dry. Indeed it seems surprising that any animals

manage to survive in it at all. These top few inches are, however, transformed by moisture, into the richest layer of the fauna. It seems possible, therefore, that with the exception of moisture, all the requirements of animals are in the upper layers throughout the period, but are not available to animals because of the extreme dryness of these upper layers. Because of this dryness, arthropods will therefore be exposed to desiccation. Desiccation is more probable in the case of arthropods living in the soil because of the etching of the wax layer which takes place in the soil (Köhler 1907). Except in soils covered with a heavy litter, humus is practically non-existent in the tropics, and the layer of food-bearing soil is extremely thin compared with the soils of more temperate regions. Animal populations will therefore be all the more concentrated, as is shown by the much greater overall density in the top 2 in.

The vertical distribution of the orders Collembola and Acarina was similar to that of the whole population. The Acarina were, with very few exceptions, free-living mites and presumably vegetable feeders. The occurrence of these two vegetarian groups in large numbers would seem to support the view put forward above, namely, that plant food is present in the top few inches, but desiccation is the deterrent to large animal populations during the dry season.

Two groups of the Arachnida, the Palpigradi and the Chelonethi, were found in the main in the lower layers and seem to be completely soil living. This is particularly obvious in the case of the Palpigradi, none of which were found in the top 6 in. If these two orders are carnivorous, they are obviously not in the optimum zone for food, at any rate in the wet season. Their distribution must therefore be controlled by some cause other than food. However, as the orders in general are retiring in habits, these particular ones are not behaving in any unusual fashion by staying in the lower layers of the soil. It is possible that desiccation in the higher layers of the soil is again the inhibiting factor.

The Pauropoda are reported to have a diet of humus and decaying plant and animal matter (Starling 1944). This agrees with their distribution with their greatest concentration in the upper layers. The Symphyla, however, are in their greatest concentration in the lower layers. Whether they are carnivorous or herbivorous, like the Palpigradi and Chelonethi, they are not at the optimum depth for food. It is possible, therefore, that again desiccation is the controlling factor.

It would appear from the above arguments, that the principal factors influencing the distribution of the soil fauna seem to be the distribution of food, and the increased possibility of desiccation in the upper layers.

Another interesting factor arising from this study, is that the season during which samples are taken, must be noted. It may be seen from the totals in each month, that the densities of animals may be three times as great in one season as in another. Comparison of the numbers of animals found in this area with the numbers found in the East African pasture (Salt 1952) shows that the density of animals is less here than in East Africa. This could be the result of many factors.

The methods used for the extraction of the arthropods are different—in East Africa the Salt & Hollick method was used; here Ladell's. There is therefore the

possibility that the two methods obtain different numbers of arthropods from the soil, and the Salt & Hollick method used in East Africa is more efficient.

Another important factor which is different in the two studies, is rainfall. In the East African work, the rainfalls, with the exception of the samples taken in the Arusha Chini district, were higher in every case than the rainfall here. If the arguments given above are true, then this could be very important in producing the higher arthropod densities in East Africa.

The amount of cover given by vegetation is important, and must be taken into consideration. The denser the cover, the less water will be evaporated from the soil below it, and therefore the more effective will be the rainfall in moistening the soil. This will be particularly so in the higher levels of the soil. It is significant that the lowest density found in East Africa by Salt was from bare ground in an area of low rainfall.

SUMMARY

1. The vertical and seasonal distribution of the Arthropoda in the top 18 in. of the soil shows an increase in the density of arthropods as the season becomes wetter.

2. This increase in density is the result of a very great increase in the density in the top 2 in. and a moderate increase in the density in the 2-6 in. layer of the soil.

3. Densities below 6 in. hardly changed as the season became wetter.

4 It is suggested that this increase is mainly due to a decrease in the danger of desiccation in the top layers of the soil.

5. There is great similarity in the proportions of the various arthropod groups in England, in East Africa and in West Africa. Important differences, however, are noted.

REFERENCES

Dammerman, K. W. (1925). First contribution to a study of the tropical soil and surface fauna. *Treubia,* **6,** 107-39.

Dammerman, K. W. (1937). Second contribution to a study of the tropical soil and surface fauna. *Treubia,* **16,** 121-47.

Glasgow, J. B. (1939). A population study of subterranean soil Collembola. *J. Anim. Ecol.* **8,** 323-53.

Köhler, A. (1907). Hemiptera. *Z. wiss. Zool.* **87,** 337-81.

Ladell, W. R. S. (1936). A new apparatus for separating insects and other arthropods from the soil. *Ann. Appl. Biol.* **23,** 862-79.

Macfadyen, A. (1953). Notes on methods for the extraction of small soil arthropods. *J. Anim. Ecol.* **16,** 65-77.

Salt, G. (1952). The arthropod population of the soil in some East African Pastures. *Bull. Ent. Res.* **43,** 203-20.

Starling, J. H. (1944). Ecological studies of the Pauropoda of Duke Forest. *Ecol. Monogr.* **14,** 291-310.

Strickland, A. H. (1945). A survey of the arthropod soil and litter fauna of some forest reserves and cacao estates in Trinidad, British West Indies. *J. Anim. Ecol.* **14,** 1-11.

Strickland, A. H. (1947). The soil fauna of two contrasted plots of land in Trinidad, British West Indies. *J. Anim. Ecol.* **16,** 1-10.

ECOLOGICAL NOTES ON THE LEMMINGS *LEMMUS TRIMUCRONATUS* AND *DICROSTONYX GROENLANDICUS* IN BAFFIN ISLAND

By ADAM WATSON

Department of Natural History, University of Aberdeen

INTRODUCTION

During the summer of 1953, the two species of lemmings *Lemmus trimucronatus* and *Dicrostonyx groenlandicus** were common in parts of S. Baffin Island, in eastern Arctic Canada. The following notes were made on the 1953 Baird Expedition which worked from May to September in Cumberland Peninsula on the east side of the island. The central area was at about 67° N in the Penny Highlands which contain the highest mountains of Baffin Island.

The biological base was 'Bio. Camp', at 180 m in Owl Valley. The valley floor, here 2-3 km wide, was very flat, banked on either side by steep mountains and ice caps rising to 1500-1800 m. This was the northern section of Pangnirtung Pass, which cuts for 100 km across the mountain belt of the peninsula. Base Camp was situated at its summit at 400 m. The southern part of the Pass, named Weasel Valley, led to a fjord and the settlement of Pangnirtung. Owl Valley was blocked to the west by the Penny Ice Cap (6000 sq. km) rising to 2000 m. To the east, two high passes cut through the mountains to the valleys June and Naksakjua, and from there to Padle Valley. This led to the east coastal fjords around Padloping Island which were visited by sledge in the early summer. There is a brief account of the climate, vegetation and topography of this area in Baird (1953).

In Cumberland Peninsula lemmings were common in all the areas visited except on the outer coast around Padloping. They were also abundant at Frobisher Bay (Sutton 1954) and in parts of Banks Island in western Arctic Canada (T. H. Manning, *in litt.*), and were reported plentiful at Clyde River, in N.E. Baffin.

NUMBERS

Large numbers were first seen in early June half way up Padle Fjord on a south-facing slope rich in heath vegetation, where there were many tracks and droppings in the fresh snow. They were then abundant at the top of the fjord and in Padle Valley, and also in Owl Valley in June. As the snow melted, hundreds of old nests appeared, built almost entirely of grasses, on the marshy floor of Owl Valley. There were very few on the hillsides, which must have been relatively deserted during the winter. Though the great majority (*Lemmus*) inhabited the wet tundra in

* The lemming binomials used are those in most frequent acceptance in the modern literature. The taxonomic position of the various closely related lemmings, still not entirely clear, has been reviewed by Rausch (1953).

the floors of the great mountain valleys, they were common on the heathy mountainsides also. Fresh nests of *Lemmus* were found to 700 m on the June River Pass, and individuals of *Lemmus* were seen occasionally up to 760 m. In July Schwarzenbach found two fresh nests of lemming (sp.?) at 980 m on the Naksakjua Pass, right at the limit of vegetation. They were built of *Luzula confusa* which grew there.

During the summer they gradually became more numerous in central Owl Valley, and were most abundant there when we finally evacuated about 20 August. They became so common that they could often easily be picked up by hand. Overnight trapping results (Table 1), all done in the same area at Bio. Camp, confirmed these field impressions. From this area of 200 × 50 yd (about 2 acres) thirty-four lemmings were removed in 2 months. The main reason for the great difference in population was certainly the appearance above ground of the peak summer generations of young in the second half of July-early August. In Alaska the peak appearance of young also came at this time (Pitelka, Tomich & Treichel 1955).

Table 1. *Trapping results, June to August*

	Traps out	Traps full		Traps out	Traps full		Traps out	Traps full
25 June	10	2	25 July	7	5	16 Aug.	4	3
29 June	10	2	26 July	7	4	17 Aug.	4	3
1 July	10	1				19 Aug.	4	4
4 July	10	2				20 Aug.	4	3
8 July	10	2						
12 July	10	3						
Totals	60	12 (20%)		14	9 (64%)		16	13 (81%)

Though there were not enough traps to make possible a proper trap line census (Elton 1942) or a census by removal of the population (Lockie 1955), the density could be roughly estimated. Traps were left unbaited outside a random selection of lemming holes containing fresh faeces. During two day periods, the traps were emptied after one day and left in the same position for another day. Sometimes a trap kept in this way caught two lemmings in two days from the same hole (e.g. seven animals caught at four holes 19-20 August). There were hundreds of holes in this area, many of them unoccupied. In late June-early July sample counts by digging and inspection for fresh excrement showed that there were over twenty holes in use for every hole in which a trap was placed. In the third week of August there were over forty. If the average number taken per trap per two day period is taken as the standard, the estimates of the population are forty in late June-early July, and 260 in the third week of August (densities of about 20 and 130 per acre). These figures can only be very roughly accurate. Lemmings may have moved in or out of the area and even the size of the area could not be determined with any precision. There was no means of estimating the effect of trapping on the population, and there may have been a bias in hole selection with such a small number of traps. Nevertheless the density could probably not have been much less than the

figures indicate. Four traps had removed about 5% of the population in only four days; if the population had been smaller, this percentage would be greater. Twenty-five traps out for five days removed less than one-quarter of the vole *Microtus* population in areas holding over 100 per acre (Lockie 1955). In early June and early July, when trapping was carried on for several days at the same holes, none were taken again from holes that had already produced a trapped individual; in late August almost as many were trapped on the second day as on the first. Thereafter no figures are available, but trapping on subsequent days may well have produced more lemmings. Unfortunately the large number of traps needed for evaluation of such factors and for an accurate check of the figures were not available. It should be noted that in this area, which lay only 100 m from the Camp, there was apparently no predation from owls or other predators. Much vegetation damage was caused in it by the lemmings. Peak density of *Dicrostonyx* at Churchill was estimated to be only sixteen per acre (Shelford 1943). This number per acre was removed by trapping alone at Bio. Camp. There must have been a high density similar to that in Owl Valley, in one area visited by Soper (1928); on one old Eskimo camp site he trapped 8 in 18 traps in one day, and a comparable frequency on succeeding days. Similarly high density was found recently during a peak in Alaska, when the average capture of lemmings in a large number of samples was forty-two per acre (Thompson 1955).

MOVEMENTS

No large-scale emigration was witnessed and there was no sign of widespread mortality which has been noticed (Rausch 1950) at times of peak abundance. A sudden movement occurred over the high Penny Ice Cap west of Owl Valley, over a low 1760 m pass in the ice dome between 22 and 25 June. W. H. Ward noticed that the numerous tracks were concentrated at the cols between glaciers flowing out N.E. and S.W. to the low country. The lemmings tended to follow ski tracks and often ran in the grooves for about 400 m. Fox (*Alopex lagopus* (L.)) tracks were also seen. Small movements probably occurred elsewhere. Though none were seen at Pangnirtung in mid-May, probably they increased or more likely moved in from elsewhere to this area, as a pair of snowy owls, *Nyctea scandiaca*, later reared a brood successfully, feeding largely on lemmings. A further change may have taken place here at the end of the summer (p. 299).

FOOD

Analyses were made of the food from mouth or oesophagus, and a few from the stomachs also, of seventeen specimens in Owl Valley, thirteen by Dr F. H. Schwarzenbach and four by the writer. These show that leaves of grasses, mostly *Poa arctica*, *Hierochloe* and *Arctagrostis*, were the most frequently eaten food. The grass leaves tend to be bitten off short and eaten from the bottom towards the apex (Schwarzenbach 1954). Many stems and roots of grasses were also eaten. Herbage, especially the blades and roots of grasses was early recorded as the

exclusive summer food of the closely related *Lemmus lemmus* in the mountains of Scandinavia (Collett 1878, 1895). The winter food contained the bark of various species of *Salix* and *Betula*. The parts of the leaves adjoining the roots were preferred by this species also. Eating of roots has also been observed in *Dicrostonyx* (Freuchen 1935, Shelford 1943) and even their storage in caches for the winter (Porsild 1937). A *Lemmus* and a *Dicrostonyx* kept in 1937 ate grass roots and the basal parts of the leaves of grasses, and tended to select *Hierochloe* from the grasses given to them (Prof. V. C. Wynne-Edwards, personal communication). Destruction of the grass in an experimental plot at Oxford was hastened by the habit of the animals (*Dicrostonyx*) of eating roots as well as stems and leaves (Elton 1942). Two of the Owl Valley specimens had also eaten some pieces of moss, and two, including the only *Dicrostonyx*, *Salix* sp. Heath plants as *Dicrostonyx* food, particularly the twigs and bark of *Salix*, and the catkins, have already been recorded in Canada, especially in winter (Sutton & Hamilton 1932, Freuchen 1935, Shelford 1943, Banfield 1951). A wide variety of summer foods of *Dicrostonyx* in the Yamal tundras of Siberia consisted mostly of heath plants such as different species of *Salix*, *Vaccinium uliginosum*, *Betula nana*, berries, fungi and others (Dunaeva & Kucheruk 1941). There was no mention of selection for any part of the plants.

FEEDING EFFECT ON VEGETATION

In July and August the well-known floor of central Owl Valley changed remarkably by the work of the lemmings. New burrows continually appeared and by mid August there was scarcely a square metre of the tundra unmarked by their activities, usually runways and burrows. The ground was littered with fresh droppings which formed a complete new mat in the densest areas. Increase in numbers was most rapid in July and early August and by the third week of August the vegetation showed easily visible evidence of serious damage by eating and burrowing. Not only were grass leaves bitten off, but great areas of the ground had become pock marked with innumerable little pits where the animals had dug for roots. The voracity of lemmings is well illustrated by an experiment at Oxford when a pair of captive *Dicrostonyx* were placed in a plot of 25 sq. yd of luxuriant vegetation. Two weeks after entry, five young were born, and in another six weeks every trace of vegetation had been destroyed (Elton 1942). Considerable wastage of food material occurs, especially grasses. Frequently the whole grass leaf may be left after the lemming has bitten it off short and eaten some. When the snow in Owl Valley melted in June it exposed lines of these cut dead grasses that had later been drifted by the wind. Similar wind rows were seen in spring in farm lands of Norway after the wintering of a migratory *Lemmus lemmus* swarm (Collett 1895), and in Alaska after a lemming peak (Rausch 1950). Rausch also noticed that there had been a marked effect on the vegetation of the tundra which was 'practically denuded' in many areas. Collett remarked that Norwegian farmers fear the lemming migrations, for this reason. No food depletion was noted in years of maximum

abundance of *Dicrostonyx* (Shelford 1943), but the density was very low (only 16 per acre).

HABITAT SELECTION

Though both species were found in the same area, *Lemmus* being greatly predominant, there was some tendency to ecological divergence in the habitats. A few *Dicrostonyx* were seen on low ground by Padle Fjord in early June before the thaw came. Two more were found dead in late June in the lower marshes of Owl Valley. These must have died in winter or early spring as they were pure white in colour. (Traces of summer coat are recorded only from April onwards in Baffin Island (Soper 1928) and north Greenland (Salomonsen 1939).) None were seen in these localities later on, but there is good evidence that *Dicrostonyx* moves to the flat lowlands in winter and returns to the dry slopes when the thaw comes (Dunaeva & Kucheruk 1941, Banfield 1951). In Owl Valley the only live *Dicrostonyx* trapped or seen after the thaw were on fairly well-drained heath on hillsides. Even there *Lemmus* occurred in far greater numbers, and extended far up the slopes, occasionally to 760 m and possibly higher, but with maximum density below 250 m. On the wet, entirely flat valley floor where they were extremely abundant, no *Dicrostonyx* was seen. Here *Lemmus* occupied even the wettest marshes, surrounded by pools and rivulets in the surface polygons. Individuals were twice observed swimming across small streams; runways have been seen that led to the water's edge (Sutton & Hamilton 1932).

That *Dicrostonyx* tends to live on high rocky ground or ridges and is not seen on flat low ground, has also been noticed near Churchill (Preble 1902), in southern Baffin Island (Soper 1928, 1944), and clearly on Southampton Island (Sutton & Hamilton 1932). Though Preble recorded that *Lemmus* was found only on low ground with deep soil, Soper and the writer also observed them in the hills. Soper suggested that though this overlap existed, no *Dicrostonyx* were taken in the lowlands where *Lemmus* was abundant. However, at our Bio. Camp not more than 15 m off the flat valley floor on a very gentle slope, several *Dicrostonyx* were seen on a stretch of wet heath where *Lemmus* was almost as common as anywhere in the valley.

The reason for such apparently conflicting observations may be that habitat selection in any one year is modified by the relative abundance of the two species. Though *Dicrostonyx* seems to prefer dry places, *Lemmus* may be found in large numbers in this habitat if *Dicrostonyx* is scarce. Probably only if both are abundant is the ecological divergence as clear cut as seen by some of these observers. In an area devoid of *Lemmus*, Shelford (1943) found that *Dicrostonyx* invaded the wet flats, typical for *Lemmus* elsewhere, only after dry seasons.

LOCAL VARIATIONS IN DENSITY

Density varied locally to a surprising extent and the difference could often not be related to obvious differences in habitat. Abundant in central Owl Valley, and lower Padle Valley, they were very much scarcer in June Valley and in lower Owl Valley. Though the lowest part of Owl Valley next to the fjord was fairly well

drained, other wet parts in the lower section, which appeared identical in vegetation and habitat to the well-populated part further up, had far fewer lemmings. Some observations on local variations in population density of *Lemmus* have been recorded on a number of islands near Cape Dorset (Soper 1928), in Alaska (Rausch 1953) where the area affected was much larger, and in Banks Island (T. H. Manning, *in litt.*).

RELATIVE NUMBERS OF *LEMMUS* AND *DICROSTONYX*

The relative numbers of the two species varied considerably in different areas. In Padle Valley all of twenty seen close in early June were *Lemmus*. In Owl Valley the great majority were *Lemmus*. Fifty-five fresh lemmings found at snowy owl nests or perches were all *Lemmus*. Analysis of a great number of owl castings from a brood in the valley showed a proportion of 946 *Lemmus* to 18 *Dicrostonyx* and two unidentified, lower jaw bones. Around the Bio. Camp, of thirty-five trapped or caught by hand there were thirty-three *Lemmus* and two *Dicrostonyx*, from an area slightly higher and drier than the wet valley floor that was most intensively quartered by the owls. Of thirty-three noted in the field in this valley, only one was *Dicrostonyx*. In the mountains, one at Base Camp and one at a glacier camp at about 1050 m were both *Dicrostonyx*. South of Base, in Weasel Valley, some fresh castings contained twenty-four *Lemmus* and two *Dicrostonyx* jaw bones. Further south at Pangnirtung, fresh castings showed a possible change with a ratio of twenty-five *Lemmus* to twelve *Dicrostonyx*. At Frobisher Bay 300 km to the south, where both species were common, *Dicrostonyx* was probably more abundant. Fresh castings collected there by Prof. V. C. Wynne-Edwards contained thirty-nine *Lemmus* and seventy-seven *Dicrostonyx* jaw bones. At Blacklead Island where numerous *Dicrostonyx* were seen by Hantzsch (1913), there were twenty-two *Lemmus* jaw bones in fresh castings, and Wynne-Edwards saw no signs of *Dicrostonyx* in the field. Kumlien (1879) also found lemmings there (about 65° N in Cumberland Sound), but the species was uncertain.

The problem of relative numbers is complicated by the fact of ecological divergence. The evidence of more *Dicrostonyx* in the southern part of Penny Highland, with a greater number at Pangnirtung and still more at Frobisher is hard to interpret. The southern valleys of the Highland were dry and heathy and so more likely to have *Dicrostonyx*. At Pangnirtung also the hillsides were fairly dry and there was no very extensive area of low wet tundra, and at Frobisher the flat land is interrupted by innumerable small rocky hills and ridges, covered with a dry heathy vegetation. On the other hand all the lemmings identified in the largely heathy June Valley were *Lemmus*. Also, though Soper (1928) recorded *Dicrostonyx* as scarce and *Lemmus* often abundant in all parts of south Baffin Island that he visited on extensive journeys, in other years *Dicrostonyx* was found by other observers to be common in some of these same areas, e.g. at Nettilling Lake (Hantzsch 1913) and Cape Dorset (Allen & Copeland 1924). At Lake Harbour, in country similar to that at Frobisher, though *Lemmus* was usually very

numerous, almost to the exclusion of *Dicrostonyx*, *Dicrostonyx* was predominant one year (Soper 1944). Soper found it very rare at Pangnirtung, but it was common there in 1953.

A few records from past years also suggest changes. In Owl Valley, counts of jaw bones were made on two old snowy owl nests, both on the same big stone, within the territory of a breeding pair. One that had been used, probably in 1952, had sixty-three *Lemmus* and six *Dicrostonyx*, suggesting a higher proportion of *Dicrostonyx* than was here in 1953. (Further evidence of a possible decline of *Dicrostonyx* since the previous year was the finding of two dead animals in winter pelage in Owl Valley in June. No *Lemmus* were ever seen dead, though they were so much more numerous in 1953.) The second nest from some earlier year had sixty-seven *Lemmus* and two *Dicrostonyx*, similar to the proportion in 1953. All the jaw bones in a sample from a large collection found in Owl River sand flats, probably a result of some catastrophic flood, were *Lemmus*. The data from here show that *Lemmus* was predominant in four different years. Most of Soper's observations in south Baffin also indicate a normal predominance of *Lemmus*. In Arctic Alaska a similar situation has been reported (Rausch 1950, Pitelka *et al.* 1955), with *Dicrostonyx* in only moderate numbers and not subject to violent fluctuations. Nevertheless in areas where *Lemmus* is normally predominant almost to the exclusion of *Dicrostonyx*, as apparently at Lake Harbour (Soper 1944), *Dicrostonyx* has been recorded as extremely abundant. At Frobisher, pellets from an old (probably 1952) owl nest contained ten *Lemmus* and seven *Dicrostonyx* jaw bones, a different ratio from 1953. Old castings at Pangnirtung had ten *Lemmus* and five *Dicrostonyx*. Some of these results are so small and few that they are offered here only as suggestions on the problem and pointers to future work. Considerably more data of this kind are needed, and I would be very pleased to examine any pellets or jaws collected or hear of any observations. The pellets are easy to keep and the lower jaws of both species, which can be easily differentiated by this means, nearly always remain intact.

It is remarkable that in two closely related species undergoing periodic cyclic fluctuations their relative numbers should vary so much within such small areas in any one year, and from one year to another in the same area. The reports on lemmings for the Canadian Arctic wild life inquiry (Chitty 1943, 1950) unfortunately did not differentiate the fluctuations of the two species. Soper (1928) suggested that the two species might alternate in abundance. Present knowledge indicates that this is unlikely, as both species may be abundant in the same area in the same year, as at Frobisher in 1953 and at Southampton Island in 1929-30 (Sutton & Hamilton 1932), and in great declines both species have been found to die (Rausch 1950). Rather the explanation may be that the two cycles are frequently not exactly in phase. It has now long been known that the cycles of northern mammals are often not synchronized over a very large area such as Baffin Island (Chitty 1950), though local variations of the kind seen in 1953 within a very small area have not been so evident. Perhaps such very local variations are more frequent where the population, as in Cumberland Peninsula, is distributed in pockets

in the deep valleys, separated by great areas of mountain and ice cap devoid of the animals.

DIMENSIONS AND WEIGHTS

Most measurements of lemming specimens in the literature are unfortunately of body dimensions only, and until recently there were very few records of weights. Clearly a combination of both is desirable. All ninety specimens from Owl Valley examined by hand appeared to be in good condition and quite fat, and there was no sign of starvation in any. Six *Lemmus*, which seemed to be full grown specimens, were weighed by calibrated spring balance at owls' nests in late June to early July (75, 80, 80, 90, 90, 95 g). Two more weighed 160 g. Fully grown *Dicrostonyx* may weigh 75 g or even 100 g (Elton 1942). Dunaeva & Kucheruk (1941) also record a

Table 2. *Measurements of Lemmings taken in Owl Valley*

			Weight (g)	Total length (mm)	Length of hind foot (mm)
Lemmus	Adult male	25 July	c. 60	141	20·0
,,	,, female	25 July	c. 70	135	19·5
,,	Immature f.	25 July	c. 35	115	18·0
,,	,, ,,	25 July	c. 30	102	19·5
,,	,, ,,	17 Aug.	32·4	112	19·5
,,	,, ,,	19 Aug.	40·4	120	19·5
,,	,, ,,	19 Aug.	36·2	115	19·0
,,	,, ,,	19 Aug.	32·6	116	19·5
Dicrostonyx	Adult ,,	19 Aug.	51·3	138	17·5
Lemmus	Immature ,,	20 Aug.	32·6	110	19·0
,,	,, ,,	20 Aug.	33·4	115	17·5
,,	,, ,,	20 Aug.	31·9	114	18·5

maximum of about 100 g in this species, and give an account of the weights of captive animals at different stages of development. Five adults, possibly not full grown, in the field in Pearyland in north Greenland weighed 42·1-53·2 g with an average of 46·8 g, and four juveniles an average of 37 g (Johnsen 1947). Many weights of both species are recorded by Rausch (1950) during a decline in Alaska, up to 95 g. In the same area, Pitelka *et al.* (1955) noted maximum weights of both species as just over 100 g. In Owl Valley the proportion of young animals increased during the summer, as those from the main midsummer generation of young appeared above ground. Animals half to three-quarters as long as adults, which must have been born about April were seen already in early June. In mid-June about one-eighth of the population consisted of such juveniles or subadults. By mid-July they totalled more than one-quarter, and about mid-August, over three-quarters of the population. A considerably more restricted breeding season was found by Pitelka *et al.* (1955) at Barrow in Arctic Alaska. Clearly the duration of breeding seasons is subject to great variation, even in the same area. In a different year at Barrow, Rausch (1950) recorded large numbers of juveniles and subadults before 12 May. On Southampton Island both species have been found to breed

throughout the year (Sutton & Hamilton 1932). There is a possibility that the duration of the breeding season is connected with the cycle in population, as suggested by Manning (1954); Rausch (1950) found no pregnancies or placental scars in summer during a population decline in Alaska. Specimens taken in Owl Valley showed the measurements given in Table 2.

SEX RATIO

It will be noted that of the eleven *Lemmus* and one *Dicrostonyx* specimens described in Table 2, only one (*Lemmus*) was a male. Of about fifty that were sexed, approximately a third were males. Unfortunately no exact notes were made. A full discussion of the problem of sex ratio in *Dicrostonyx* (Manning 1954) is equally relevant to *Lemmus*.

PREDATORS

Apart from snowy owls, *Nyctea scandiaca*, which fed almost entirely on lemmings, predators were rare. Foxes, *Alopex lagopus*, and stoats, *Mustela erminea*, were rare at Frobisher (Sutton 1954) and at Pangnirtung and Penny Highland. In Owl Valley no stoats and only one fox were seen. There were a small number of ravens, *Corvus corax*, in all these areas, but very few away from the settlements. No jaegers, *Stercorarius*, were seen in Penny Highland and no rough-legged buzzards, *Buteo lagopus*, though a few buzzards were breeding at Frobisher according to Prof. V. C. Wynne-Edwards. Falcons, both Greenland, *Falco rusticolus*, and peregrine, *F. peregrinus*, were rare in Penny Highland and no nests were found in Owl Valley. The density of snowy owls, *Nyctea scandiaca*, was well correlated with lemming density. There were no owls in June Valley, Kingnait Pass and the upper and lower parts of Owl Valley where lemmings were scarcer. In the densest lemming ground in middle Owl Valley six owl pairs each had territories of about one square mile and broods of from seven to nine young were reared successfully. Territories were also of this size in Padle Valley where lemmings were very abundant in early June and in August. Lower down Owl Valley where lemmings were scarcer, only one pair of owls was found in about 8 miles of valley, with a territory of at least 3-4 square miles and a brood of six young in mid-July. A similar variation in territory size with local abundance of prey was found in jaegers, and short-eared owls, *Asio flammeus*, in Arctic Alaska (Pitelka *et al.* 1955).

DISCUSSION

Though the snowy owls took a heavy toll of lemmings in Owl Valley (the exact quantities affected to be reported elsewhere), and were able to rear broods of 7-9 young to fledging time, this predation had little eventual effect on the lemming population, which increased rapidly throughout the summer. On the other hand avian predation in summer was believed to have dealt a 'stupendous blow' to the lemming population in an area of Arctic Alaska (Pitelka *et al.* 1955). In spite of the great production from the summer generation of young, lemming numbers in mid-July were reported to have been reduced to one-tenth, one-twentieth or even less,

of those existing in early to mid-June on the melting of the snows. This was found not by direct quantitative observations, but by deduction from the density and food consumption of the predators. Shelford (1943), who also noted that predators do reduce significantly the numbers of lemmings at Churchill when these are abundant, refers to 'positive evidence' of this. Predation in Alaska was very heavy, particularly from large numbers of breeding jaegers, *Stercorarius*, and short-eared owls, *Asio flammeus*. There was evidently considerable competition for prey, and the breeding success of snowy owls was extremely low compared with that found in Owl Valley. The clutch size was also lower (clutches in Owl Valley 7-9, average 8). In this species clutch size appears to vary according to the abundance of rodent and other food. An additional factor may well be the relative accessibility of the supply, depending on the amount of competition from other predators utilizing the same food.

In fact the impact of the predators, and the pattern of the predator-prey cycles of the type idealized by Gause (1934), which this case slightly resembles, probably vary from one part of the Arctic to another, depending mainly on the number of nomadic predators that happen to assemble, the relative efficiency of their predation, the state of the prey cycle, and the breeding rates of both predators and prey. Resident predators probably have the greatest effect on the prey when the latter have already been reduced by other means. A wide variation is possible. Where the only predators are resident they cannot breed fast enough to have a proportional effect on the increasing rodent population (Elton 1926, Haldane 1953). The situation in Owl Valley, though different in origin, had a similar effect; the resident predators were rare and the nomadic predators were not present in strength sufficient to control the numbers of prey. The lemmings increased out of proportion to the maximum demand of the snowy owls feeding without competition, and the result was severe damage to the vegetation. In the case studied by Pitelka *et al.* (1955), the nomadic predators assembled in such numbers that the rising prey population was unable to increase fast enough to meet their demand in the breeding season. Not even able to sustain its original numbers, the population was believed to have been reduced to a minute fraction of its size before heavy predation started.

The toll of the avian predators in this area of Alaska was considered so high that there could be no danger of undue exploitation of the vegetation by the lemmings. Clearly such a conclusion can not have general application as the above discussion demonstrates. During vole, *Microtus*, plagues also, the vegetation may be heavily damaged (Adair 1893). Lack (1954) has suggested that food shortage may be the initial cause of the decline in numbers of both lemmings and voles. The damage in parts of Owl Valley was so great as to suggest that even a delayed density-dependent effect on the lemming population might result in the absence of disease or emigration. Nevertheless lemming specimens taken in the third week of August in areas showing serious vegetation damage were all in good condition and quite fat, and no dead or sick individuals were seen. In Alaska, Weber (1950), who observed damage of the vegetation during a lemming decline, wrote that they

destroyed so much of the slow-growing vegetation that they eventually starved. Rausch (1950) who also witnessed destruction of vegetation during this decline, but made observations over a longer period before and after it, disagreed with this conclusion: he had found nothing tangible to indicate death by starvation. During a vole peak and decline in Wales, Chitty (1952) also found that the animals were at maximum weight and showed no signs of starvation.

Emigration or decline in numbers may at least be postponed until after the vegetation shows considerable damage (e.g. Owl Valley in 1953, Rausch 1950). Unfortunately we could not stay any longer in Owl Valley to see what happened later. In other places, e.g. Pangnirtung, there is a suggestion that the lemmings had declined in number by the autumn or that many had moved. In early September the vegetation in general showed no great damage there and lemmings were scarcely seen. A pair of snowy owls had reared a brood, but left very early with their newly-fledged young in the third week of August. Other owls were on the move before the end of August through Owl Valley also. Several adults appeared at that time and there were serious fights with the local resident owls. There may have been a greater decline in numbers later, as numerous snowy owls appeared in southern Canada and in the United States the following winter (W. E. Godfrey, *in litt.*).

Unlike the nomadic snowy owls which probably usually find some part of the Arctic where lemmings are common, and probably do not migrate south unless there is a widespread decline in the numbers of prey, foxes and weasels cannot travel so extensively. When the lemmings become scarce, they probably prey more on other animals, especially ptarmigan, *Lagopus mutus*, and hares, *Lepus timidus* L. As both are generally far less common than lemmings, such a shift in predation is likely to have a marked effect on their populations. Both Elton (1942) and Lack (1954) suggested explanations of the cycles of ptarmigan in this way. The fact that in south Baffin Island all the resident predators and both main secondary prey species, hares and ptarmigan, were generally uncommon is suggestive. The only places where hares and ptarmigan were seen in any numbers were on the outer Padloping coastal areas where lemmings were scarce in 1953, and where even old signs of lemming activities were only infrequently seen. At Frobisher Bay the decrease of lemmings had probably taken place by the summer of 1952. No lemmings were seen then on the southern coast of the bay by Blake (1953). The predators had also decreased: no snowy owls or foxes were seen, and though the ptarmigan were still plentiful, there were no hares. Foxes were very scarce at Frobisher Bay in January 1953 according to R.C.M.P. Constable R. D. Van Norman. Though ptarmigan were still plentiful then, in mid-May they were not so common, probably decreasing, and were found scarce in the summer by D. V. Ellis who worked in this region for some weeks. Decrease in numbers of the gallinaceous bird after the hare has been recorded a number of times (Lack 1954).

In Bylot Island, north of Baffin, lemmings had 'crashed', and were very rare in the summer of 1954 (J. Van Tyne, *in litt.*). Many old snowy owl nests were found but only one live owl, and ptarmigan were scarce, a similar situation to that at

Clyde Inlet in N.E. Baffin Island in 1950 (Wynne-Edwards 1952). More correlative observations of this kind are needed. Though well understood in the subarctic, the fluctuations of ptarmigan and hares are still little known in the high arctic, and there is even less positive observation on the state of the lemming cycles in relation to them.

The interrelations of the two lemming species also require further observation. The relative numerical proportion each species forms of the total lemming population varies so greatly within the same area from year to year that the two populations must clearly be subject to some difference in environmental forces. An analogous case has been suggested to me by Prof. V. C. Wynne-Edwards in the closely related arctic redpolls *Acanthis flammea* and *A. hornemanni*. Their relative numerical proportions also appear to vary in the same area from year to year (Grinnell 1943 and other unpublished observations).

ACKNOWLEDGMENTS

I am very grateful to F. H. Schwarzenbach for his analysis of the food of some lemming specimens. Other members of the expedition gave useful notes on their observations. T. H. Manning kindly let me see part of some manuscripts on the birds of Banks Island. Some suggestions on preparing this paper were made by Prof. V. C. Wynne-Edwards.

SUMMARY

1. The lemmings, *Lemmus trimucronatus* and *Dicrostonyx groenlandicus*, were abundant in parts of Baffin Island in 1953.

2. There was considerable local variation in numbers, even within one valley. A tendency to a specific difference in habitat selection was noticed, with *Dicrostonyx* preferring dry heathy slopes. The relative abundance of the two species varied greatly in different parts of the island, and also in the same area from year to year. Their population fluctuations are apparently often independent or not in phase.

3. In one valley there was a great increase of *Lemmus* during the summer, mainly due to the peak appearance of young in July. An estimate of the population density was made in one small area.

4. By late August the vegetation over a large area in one valley showed serious damage by lemming eating and burrowing. Leaves and roots of grasses were the usual summer food of *Lemmus*. There was a great wastage of food material.

5. There was some local movement of lemmings but no widespread emigration.

6. No signs of disease or starvation were detected, and specimens were all in good condition.

7. Snowy owls (*Nyctea scandiaca*) were common and reared large broods fed almost entirely on lemmings. Their density was closely correlated with lemming density.

REFERENCES

Adair, P. (1893). Notes on the disappearance of the short-tailed field vole (*Arvicola agrestis*), and on some of the effects of the visitation. *Ann. Scot. Nat. Hist.* 1893, 193-202.

Allen, G. M. & Copeland, M. (1924). Mammals from the MacMillan Expedition to Baffin Land. *J. Mammal.* **5,** 7-12.

Baird, P. D. (1953). Baffin Island Expedition, 1953 : A preliminary field report. *Arctic,* **6,** 226-51.

Banfield, A. W. F. (1951). Notes on the mammals of the Mackenzie district, Northwest Territories. *Arctic,* **4,** 112-21.

Blake, W. (1953). Studies of the Grinnell Glacier, Baffin Island. *Arctic,* **6,** 167.

Chitty, D. (1952) Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-39. *Philos. Trans.* (B) **236,** 505-52.

Chitty, H. (1943). Canadian Arctic Wild Life Enquiry, 1941-42. *J. Anim. Ecol.* **12,** 163-72.

Chitty, H. (1950). Canadian Arctic Wild Life Enquiry 1943-49: with a summary of results since 1933. *J. Anim. Ecol.* **19,** 180-93.

Collett, R. (1878). On *Myodes lemmus* in Norway. *J. Linn. Soc.* (Zool.) **13,** 327-34.

Collett, R. (1895). *Myodes lemmus;* its habits and migration in Norway. *Forh. Videnskselsk. Krist.* **31,** 1-62.

Dunaeva, T. & Kucheruk, V. (1941). [Material on the ecology of the terrestrial vertebrates of the tundra of south Yamal.] *Bull. Soc. Nat. Moscou.* (N.S., Zool. Sect.) **4,** (19), 1-80 (in Russian ; translation at Bureau of Animal Population, Oxford).

Elton, C. (1926). *Animal ecology.* London.

Elton, C. (1942). *Voles, mice and lemmings.* Oxford.

Freuchen, P. (1935). Mammals. Part 2. Field notes and biological observations. *Report of the Fifth Thule Expedition 1921-24.* Vol. **2,** 68-278. Copenhagen.

Gause, G. F. (1934). *The struggle for existence.* Baltimore.

Grinnell, L. I. (1943). Nesting habits of the common redpoll. *Wilson Bull.* **55,** 155-63.

Haldane, J. B. S. (1953). Animal populations and their regulation. *New Biology,* **15,** 9-24.

***Hantzsch, B. (1913).** Beobachtungen über die Säugetiere von Baffinsland. *S.B. Ges. naturf. Fr. Berl.* 1913 (2), 141-60. (Translation by M. B. A. & R. M. Anderson 1927 in Nat. Mus. Can.)

Johnsen, P. (1947). Birds and mammals of Peary Land in North Greenland. *Medd. Grønland,* **128** (6), 1-140.

Kumlien, L. (1879). Contributions to the natural history of Arctic America, made in connection with Howgate Polar Expedition, 1877-78. *Bull. U.S. Nat. Mus.* **15,** 1-179.

Lack, D. (1954). *The natural regulation of animal numbers.* Oxford.

Lockie, J. D. (1955). The breeding habits and food of short-eared owls after a vole plague. *Bird Study,* **2,** 53-69.

Manning, T. H. (1954). Remarks on the reproduction sex ratio and life expectancy of the varying lemming, *Dicrostonyx groenlandicus,* in nature and captivity. *Arctic,* **7,** 36-48.

Pitelka, F. A., Tomich, P. Q. & Treichel, G. W. (1955). Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr.* **25,** 85-117.

***Porsild, A. E. (1937).** *Edible roots and berries of Northern Canada* (in Nat. Mus. Can.)

Preble, E. A. (1902). A biological investigation of the Hudson Bay region. *N. Amer. Fauna,* **22,** 1-40.

Rausch, R. (1950). Observations on a cyclic decline of lemmings (*Lemmus*) on the Arctic coast of Alaska during the spring of 1949. *Arctic,* **3,** 166-77.

Rausch, R. (1953). On the status of some Arctic mammals. *Arctic* **6,** 91-148.

Salomonsen, F. (1939). Moults and sequence of plumage in the rock ptarmigan (*Lagopus mutus* (Montin)). *Vidensk. Medd. naturh. Foren. Kbh.* **103,** 1-491.

Schwarzenbach, F. H. (1954). A botanist in Arctic mountains. *The Mountain World,* 163-8. Swiss Foundation for Alpine Research.

Shelford, V. E. (1943). The abundance of the Collared Lemming (*Dicrostonyx groenlandicus* (Tr.) Var. *richardsoni* Mer.) in the Churchill area, 1929 to 1940. *Ecology* **24,** 472-84.

* Not seen in the original.

Soper, J. D. (1928). A faunal investigation of southern Baffin Island. *Bull. Nat. Mus. Can.* **53,** 1-143.

Soper, J. D. (1944). The mammals of southern Baffin Island, N.W.T., Canada. *J. Mammal.* **25,** 221-54.

Sutton, G. M. & Hamilton, W. J. (1932). The mammals of Southampton Island. *Mem. Carneg. Mus.* **12,** (2), 1-111.

Sutton, G. M. (1954). Nesting of the snow bunting on Baffin Island. *Wilson Bull.* **66,** 159-79.

Thompson, D. Q. (1955). The 1953 lemming emigration at Point Barrow, Alaska. *Arctic,* **8,** 37-45.

Weber, N. (1950). The role of lemmings at Point Barrow, Alaska. *Science,* **111,** 552-53.

Wynne-Edwards, V. C. (1952). Zoology of the Baird Expedition (1950). 1. The birds observed in central and south-east Baffin Island. *Auk,* **69,** 353-91.

A PRELIMINARY EXPERIMENT ON THE LOCAL DISTRIBUTION OF BLOWFLIES

By JOHN MACLEOD

Ministry of Agriculture (Animal Health Division), Field Research Laboratory, Blackford, Carlisle

(With Plate 1)

Where a naturally occurring population of a small mobile organism is being sampled, it is almost invariably necessary to accept a biassed sample, even though no attracting device is employed. Sweeping the vegetation, for example, results in an unavoidable bias in that the sweep of the net is checked by obstacles, and organisms sheltering on or near such obstacles will tend to escape capture. Even on smooth ground the chance of capture of an individual resting in or on the vegetation is affected by its relative accessibility, and its agility. Similarly, sampling by suction fans selects the airborne fraction for sampling.

Since bias is almost unavoidable, it must be allowed for, and therefore it is immaterial whether the degree of bias be high or low, provided the correction factor is known. This is the justification for attractant devices in sampling.

It is, however, frequently easier to obtain the correction factors for patently biassed samples than for those which have a deceptively random appearance. With light-trapped samples, for example, no serious analysis would omit to include the effect of meteorological conditions on the catch, whereas the less obvious distortion of a sweep-net sample might be omitted from consideration, because of the difficulty of measuring it.

In the diptera, the carrion-infesting blowflies form a group which because of the range, strength and speed of their flight are difficult to sample randomly; they lend themselves admirably however to the method of sampling by carrion-baited traps. Much work has still to be done on the effect of physiological variables, *e.g.* recent feeding- or activity-history, degree of maturity of the females, and such, as well as of weather factors, on the response of blowflies to standard bait, but even lacking such knowledge the results of simultaneous samplings are in themselves of value for comparative work, since the compared population can be regarded as that proportion of the population which is able and willing to respond to the bait stimulus. It is natural to assume in such case that differences can be related to differences in treatment, the 'effective' population in a limited uniform area at a given moment being assumed to be homogeneous.

On this basis, a replicated test was made of the treatment effect on blowfly catch of raising the baited trap 3 ft above ground level. The matter was regarded as a minor point of technique in a projected study of blowfly ecology, arising from the

possibility of interference with the traps by wild animals. In the outcome, the question was not clearly settled, and has since been lost sight of in the progress of the main work. The failure is accounted for by the experimental demonstration of quite unsuspected sources of variability in sampling by this method. The experiment is analysed in detail below mainly because of this incidental revelation, which, among other results, destroys the validity of the assumption, outlined above, that for simultaneously obtained samples, under similar conditions, the 'effective' blowfly population is homogeneous for different traps.

From the point of view of this work, expected sources of variation attached to the traps might perhaps be classified thus:

Even hypothesizing truly identical traps and bait portions, there would still of course be purely chance differences in the catches, from chance or conditioned variations in the density distribution of flies in space, *i.e.* true random variation.

In practice, in a set of apparently identical traps, baited with meat portions which appear to the experimenter to be similar, and distributed over an ecologically uniform area, there will usually be additional differences in catch due to undetectable differences between bait portions, and trap differences, *e.g.* in surface reflection, contamination by flies, residual organic odours, and such.

In addition to these insidious sources of heterogeneity — the un-measurable 'treatment' differences — there are obvious but equally unescapable 'treatment' sources of disturbance in the effect of adjacent traps one on another, since a fly caught in A is denied to the adjacent B into which it might otherwise have gone, and the unavoidable difference in position (one trap must always be west or south of, or above, the other).

The last two are 'treatment elements' in the variance, but since they are in practice inseparable from the error variance of grouped traps they are normally included in this. In the following analysis it has been possible to examine in some detail the effect of relative position, both horizonal and vertical. The unexpected and important result is the demonstration of a distinct effect on catch of 'relative trap position' — the position occupied by a trap in relation to the others of the group, when all the traps are in an apparently uniform fly habitat.

In this, and all related work, the catch consisted of *Lucilia* spp., *Calliphora erythrocephala* (*C.e.*), *C. vomitoria* (*C.v.*), *Phormia terrae-novae* (*P.t-n*) and *Cynomyia mortuorum* (*Cyn.*), plus Sarcophagids, occasional *Pollenia*, and Muscids. These latter three groups are not included in the listed results. The *Lucilias* were *L. sericata* (*L.s.*), *L. caesar*, *L. illustris* and *L. ampullacea*. The latter three, in this preliminary experiment, were identified merely as *L. caesar* group (*Lc.*gp.); they may have included a limited number of *L. silvarum*. (For brevity, subsequent reference to the species will be made by the initials indicated in brackets.)

The experiment was set up in May 1949, on the war-time aerodrome of Crosby, north of Carlisle. Five pairs of trap stands were arranged around the laboratory in a rough circle of some 50 to 70 yd diameter. The terrain is illustrated in the photograph (Pl. 1, A). The trap-stands were erected so as to project 3 ft and 9 in. respectively above ground level, and the traps securely held in position on these.

the Crosby laboratory, on which the experimental pairs

B. Position 3, showing the two stands, 9 ft apart. June trapping, 1950. The traps are in an agrostetum-holcetum, and the adjoining field was on this occasion under oats.

Table 1. *Total Calliphorines caught in high (H) and low (h) traps*

Position		I		II		III		IV		V		Total	
Day		H	h	H	h	H	h	H	h	H	h	H	h
May 1949	1	2	15	2	11	3	0	4	42	3	18	14	86
	2	3	15	5	1	4	0	7	30	6	31	25	77
	3	0	9	2	0	14	2	6	15	15	33	37	59
	4	0	13	0	2	6	4	1	26	11	31	18	76
	5	0	3	0	2	0	0	1	0	0	1	1	6
	6	3	70	3	3	4	20	5	17	4	6	19	116
	7	0	6	1	0	0	1	0	4	0	1	1	12
Total		8	131	13	19	31	27	24	134	39	121	115	432
July 1949	1	44	53	37	61	4	24	22	18	26	10	133	166
	2	103	184	108	150	91	84	63	191	32	61	397	670
	3	74	55	31	11	15	13	15	18	14	28	149	125
	4	36	36	30	6	9	13	8	3	16	8	99	66
	5	32	30	14	1	4	4	7	0	22	13	79	48
Total		289	358	220	229	123	138	115	230	110	120	857	1075
Oct. 1949	1	80	40	59	30	27	22	44	4	4	22	214	118
	2	60	27	159	19	90	4	50	62	101	256	460	368
	3	82	83	119	11	159	9	62	73	116	175	538	351
	4	5	8	10	6	3	2	8	0	18	18	44	34
	5	43	7	14	15	41	3	47	12	48	23	193	60
Total		270	165	361	81	320	40	211	151	287	494	1449	931
June 1950	1	39	0	0	16	7	10	23	16	4	10	73	52
	2	18	44	5	5	2	4	45	37	7	15	77	105
	3	14	11	1	1	1	0	11	0	2	9	29	21
	4	5	17	2	1	0	3	8	11	4	13	19	45
	5	1	6	0	1	2	0	1	3	2	6	6	16
Total		77	78	8	24	12	17	88	67	19	53	204	239
Sept. 1950	1	18	92	16	16	7	15	8	1	6	12	55	136
	2	3	35	0	2	1	4	12	1	4	12	20	54
	3	21	16	10	7	4	5	8	2	6	3	49	33
	4	17	45	10	11	7	5	14	5	7	16	55	82
	5	20	148	18	37	13	20	30	60	10	53	91	318
Total		79	336	54	73	32	49	72	69	33	96	270	623
June 1951	1	33	33	10	7	3	8	29	15	16	16	91	79
	2	17	14	1	4	6	1	7	7	5	4	36	30
	3	52	40	12	8	29	14	62	23	37	13	192	98
	4	12	15	21	6	42	7	16	4	7	4	98	36
	5	6	5	7	1	12	3	7	1	4	2	36	12
Total		120	107	51	26	92	33	121	50	69	39	453	255
Oct. 1951	1	142	73	24	52	60	86	74	81	15	9	315	301
	2	192	168	43	124	192	205	204	129	30	50	661	676
	3	50	31	23	20	22	11	21	18	16	5	132	85
	4	150	350	90	250	170	116	177	158	197	216	784	1090
	5	159	68	100	130	90	57	102	80	130	47	581	382
Total		693	690	280	576	534	475	578	466	388	327	2473	2534
Grand total		1536	1865	987	1028	1144	779	1209	1167	945	1250	5821	6089

The stands of each pair (Pl. 1, B) were 9 ft apart. The traps were baited with similar portions of rabbit, and trapping continued for seven consecutive days, the traps being changed daily, and the bait renewed once, on the fourth day. Another series of comparisons, for five days only, was made in July and again in October, with these five pairs of trap-stands, the bait being changed on the third day.

The traps used, a cylindrical gauze-walled type, were all apparently identical, but each day's replacement represented a different set of ten, from the available stock of 100 replicates; thus catch variation within a trapping series is free from the complication of recurrence of idiosyncrasy of any individual trap.

The ratios of total Calliphorines caught in the high and low traps (H : h) were 1 : 4 in May, 4 : 5 in July and 3 : 2 in October. This variability was not obviously related to the species composition; in May and October the catch was almost entirely *C.e.*, yet these two series showed the greatest catch disparity between heights.

The experiment was repeated in 1950, using the same stands and method, and five-day replications. In order to get species other than *C.e.*, the seasonal range was shortened, the trapping series being in June and September. A height disparity again occurred in the late season series but this time in favour of the low stands. The early season series showed little difference, but the catches were low. The experiment was repeated in June and the first week in October 1951, and, in the hope of improving the catch numbers, fish was used for bait. An early season disparity in favour of high stands was followed by a nil difference in the late season total, when the catch was again preponderantly *C.e.* Thus, after three years, no clear-cut conclusion could be drawn from inspection of the totals.

The catches for each trap occasion are given in Table 1. In the first series, days 5 and 7 gave negligible catches, and, to make the series uniform for mathematical handling, they have been omitted from later tabulations, with the exception of the final analysis (Table 9).

Sex appeared to have no effect on the distribution of the species between high and low traps: the sex-ratio (males : females) of the total catch of *Lc.*gp. and *C.e.* over six series (excluding October 1949) was almost the same for both trap levels:

	*Lc.*gp.	*C.e.*
H.	1 : 21·2	1 : 23·6
h.	1 : 20·5	1 : 23·8

Table 2 compares the total high and low trap catches for species for each series. In the October 1949 series, the *Calliphora* species were not separated. For analysis purposes the total for this series has been apportioned to *C.e.* and *C.v.* in the ratio 7 : 1, the ratio obtained in independent trappings carried out on the aerodrome at that time. The ratio *Lucilia* : *Calliphora* included in Table 2 is a measure of the extent to which the bait-trap population contained species other than *C.e.*, the principal species.

The table shows that, for each series, the H : h ratio is not related to the *Lucilia* : *Calliphora* ratio; in the *Lc.*gp., however, the ratio is fairly consistently low, whereas with *C.e.* it has an irregular bias for high stands. When the totals for

Table 2. *The effect of height on the catch of each species*

Series commencing		*L.s.*	*Lc.* gp.	*C.e.*	*C.v.*	*P.t-n/Cyn.*	*Total*	Luc : Call.	H : h.
10 May 1949	H	0	0	113	0	0	113	(All *C.e.*)	1 : 4
	h	1	1	396	3	13	414		
25 July 1949	H	24	79	714	11	29	857	5 : 13	4 : 5
	h	61	363	593	35	22	1074		
6 Oct. 1949	H	6	28	1219	174	22	1449	1 : 30	3 : 2
	h	2	24	783	112	10	931		
12 June 1950	H	6	86	103	4	5	204	3 : 2	5 : 6
	h	6	153	64	4	12	239		
4 Sept. 1950	H	0	53	199	7	11	270	1 : 2	3 : 7
	h	1	213	354	35	20	623		
18 June 1951	H	4	34	408	1	6	453	1 : 6	9 : 5
	h	0	66	182	2	5	255		
1 Oct. 1951	H	0	59	2169	230	15	2473	1 : 30	1 : 1
	h	0	94	2200	231	9	2534		
Total	H	40	339	4925	427	88	5819	1 : 8	
	h	71	914	4572	422	91	6070		
YEAR TOTALS									
1949	H	30	107	2046	185	51			
	h	64	388	1772	150	45			
1950	H	6	139	302	11	16			
	h	7	366	418	39	32			
1951	H	4	93	2577	231	21			
	h	0	100	2382	233	14			

the two main species, over the six series (i.e. excluding the nil *Lc.*gp. May series), are compared for height in a fourfold table, the χ^2 for contingency is, as would be expected from inspection, extremely high. It is obvious that the effect of height is more pronounced with *Lc.*gp. than with *C.e.*, but, perhaps less obviously, the χ^2 for difference in the *C.e.* catches is also high (45.3); assuming independence of the observations, this is overwhelmingly significant.

*Lc.*gp.: H 339, h 913; *C.e.*: H 4814, h 4176; deviation from expectation 291; χ^2 (1 df) 134+136+18·7+18·9.

When classified by season, confounded for year (Table 3), the series totals make no clearer picture; there is no obvious season effect on the H : h ratio for the species groups.

Clearly the effect of height on the size of catch of bait-trapped calliphorines is not a straightforward quantitative or even qualitative difference. The species pattern of the calliphorine population being sampled is, apparently, one interacting variable; the possibility of the other two main variables, time and position, being also capable of altering the effect of height was next tested, by examining the day to day results in each series, for the individual pairs of traps in Table 1.

Because of the high variance of the differences in pairs of traps, the mean difference, for a given day or a given pair, cannot usefully be examined by 't' test. Thus no day of the first two series shows significant differences between high and low traps over the five positions when the raw data are tested by the 'correlated pairs' method. Even more surprisingly, position I, in series 1 trapping (May), with a

(5-day) total 8 to 122, each day being consistently better for low trap, is not significant; the mean difference of 23 is barely twice the standard error.*

The χ^2 measure of variation is applicable to the majority of the results (total Calliphorines), although in two series, May 1949 and June 1950, the catches were frequently too low for the test to be reliable.

The χ^2 for the two pooled catches (H and h) in a given group measures the nett bias for height of the group as a whole; the summed χ^2s for individual pairs give a measure of the gross, or total, deviation from equality between the high and low traps of a group. This gross χ^2 will be greater than the χ^2 for the totals, the difference, the heterogeneity component, representing that part of the gross χ^2 which

Table 3. *Trap height and catch in relation to season*

		L.s.	*Lc. gp.*	*C.e.*	*C.v.*	*P.t-n/Cyn.*	Total
June	H	10	120	511	5	11	657
	h	6	219	246	6	17	494
July	H	24	79	714	11	29	857
	h	61	363	593	35	22	1074
September	H	0	53	199	7	11	270
	h	1	213	354	35	20	623
October	H	6	87	3388	404	37	3922
	h	2	118	2983	343	19	3465

is due to inconsistency in direction of individual differences, due either to interaction or merely to chance irregularity. The relative size of this and the homogeneity component, the nett bias, will indicate the extent to which the gross difference is due to a trend.

For each series the total χ^2 and its homogeneity and heterogeneity components were calculated for each day over the five positions, and for each position over the five days. The results are given in Table 4. Except where indicated by a suffix letter for height, the homogeneity χ^2 indicates a deviation in the direction suggested by the distribution.

The 'pooled' column for positions gives the homogeneity and interaction components of the χ^2 for the series, regarding the day totals over all positions as the observations; the 'pooled' column for days similarly uses the position totals. The heterogeneity component has 4 degrees of freedom and involves the additive use of χ^2; the Yates correction for the bias of enumeration data cannot therefore be applied. This omission however is not important here, as no precise probability estimate is being derived.

Because of the discrepancies between pairs in the direction of the bias, the question arises whether the differences between the high and low traps may not be merely an effect of two adjacent traps one on another, and not a height effect at all. It is clear that, since the same fly cannot go into two traps, flies arriving from some distance must exercise selection even with replicate traps.

* Mr J. G. Skellam points out that, if no assumption is made about normality, then the probability that the h value exceeds the H value on all 5 occasions (Position I, Series 1), is $(\frac{1}{2})^5$, making the obtained result clearly significant. He goes on: 'We obtain a significant result also by the t-test if we transform the data first. But in doing so we have to assume that the "form" of the sample is a sufficiently good guide to the "form" of the universe to enable us to find a reasonably satisfactory normalizing transformation. In this case I think that such an assumption can be justified.'

Significance of differences within pairs and of the heil bias of grouped traps

Series	χ^2	Positions I H	Positions I h	Positions II H	Positions II h	Positions III H	Positions III h	Positions IV H	Positions IV h	Positions V H	Positions V h	Pooled H	Pooled h	Days 1 H	Days 1 h	Days 2 H	Days 2 h	Days 3 H	Days 3 h	Days 4 H	Days 4 h	Days 5 H	Days 5 h	Pooled H	Pooled h
I	++		5			1	1		4		4		4		3		3		1		3		3		3
	+				1				1				1		1				1						
	N.S.					1				1															
	?			4		2								1		2		1		1		1		2	
	Homogeneity	100		0·9		0·4$_H$		74·8		40·5		172		51·8		26·5		5		35·8		69·7		172	
	Heterogeneity	2·8				26·7		4·5		3·8		17		10·8		19·4		25·7		12·2		9·5		44·5	
II	++		1	3	1		1		1	1	1	1	1	1	1		4	1		1		1			2
	+				1					1		1			1				1						
	N.S.	4				3		3		2		2		2		1		3		4		1		3	
	?					1		1														3			
	Homogeneity	7·37		0·18		0·86		38·3		0·43		24·6		3·64		70·6		2·1		6·6		7·56		24·6	
	Heterogeneity	20		51		11·6		36		25		66		25		36		15		17		13·65		66	
III	+	3		3		3		2		1	3	4		3	1	3	1	2	1			4		4	1
	+																								
	N.S.	2		2		1		2		1		1		1		1		2		3		1			
	?					1		1												2					
	Homogeneity	25·5		177		247		10		55		113		28		10·2		39		1·28		69		113	
	Heterogeneity	27·1		34		30		54		52		568		40		261		204		8·6		19·8		373	
IV	++	1	1		1			1					1	1	1		1	1							2
	+		1							2		2							1		2				
	N.S.	1		1		1		3		2		2		3		3		1		1				3	
	?	1		3		4		1		1						1		2		2		5			
	Homogeneity	0·01		8		0·86$_h$		2·84$_H$		16		2·76		3·5$_H$		4·3		1·28$_H$		10·6				2·76	
	Heterogeneity	60						11·7		0·7		113		56		11		15·5		4·5				25	
V	++		4					1	1		1		3		1	1	1				1		3		2
	+				1			2			1		1	1			1			1			1		
	N.S.	1		3		3			2		1			3				3		3		1		3	
	?			1		2		1		1						2		2							
	Homogeneity	160		2·83		3·57$_h$		0·06		31		140		31·3		15·6		3·12$_H$		5·32		128		140	
	Heterogeneity	28		6·3		3·06		32		8·5		138		26		28·5		2·8		15·45		17		57	
VI	++		1		1		1	2		1		3						2		3				4	
	+					2		1						1				1				1			
	N.S.	5		2		1		1		2		2		4		2		2		2		1		1	
	?			2		1		1		2						3						3			
	Homogeneity	0·75$_H$		8·13		28		29		8·3		55·4		0·85		0·56$_H$		34		29		12		55·4	
	Heterogeneity	1·5		7·8		13		4·95		4·8		52		6·4		5·21		3·92		12·7		3·16		19	
VII	++	2	1		3	2		1		1	2	1		1	1	1	1			1	2	3		1	1
	+	1			1	1	1			1	1				1		1	2					1	1	
	N.S.	1		1		1		4		2		2		2		2		3		2		1		2	
	?																								
	Homogeneity	0·01		102		3·48		12		5·2		0·74$_h$		0·32$_H$		0·17		10·2		50		42		0·74	
	Heterogeneity	144		26·4		23		9·2		47		371		38		62·5		4·13		117		47		122	

++ = Significant on 1% basis. N.S. = Not significant by χ^2 test.
\+ = Significant on 5% basis. ? = Not entered, as numbers too low.

With high densities of local flies, an appreciable proportion will be within the zone of influence of individual traps from the beginning of response, and their distribution among traps will tend to reflect the relative attractiveness of the traps, but with lower local populations, much of the catch represents flies drawn by the common 'pull' of two adjacent traps. On arrival near the pair, these flies may have their choice determined not by height but by such accident as the number of flies already present. There may thus be a 'trap contiguity' effect, which will tend to produce differences in adjacent pairs.

It is difficult to separate this source of variation from possible position differences, but there are two indications from the results that the effect does not account for most of the observed differences. Thus, a trap contiguity effect should be randomly distributed for height, but the homogeneity χ^2 for any given day is usually significant, suggesting a basic consistency of bias, and the heterogeneity component is more often due to differences in scale of the height bias between positions on that day than to qualitative differences in height response. Secondly, the differences associated with height are not more pronounced on days of high catch than when a low total number is caught. The results have therefore been examined on the assumption that the differences are associated with the treatments.

Inspection of the table shows that the H : h discrepancies between series totals are not due to differences in species composition of the catches (cf. series 1, 3 and 7, with almost pure *C.e.*). With each series, the H : h ratio varied between positions, the interaction showing as a significant and often high heterogeneity χ^2 for at least four days in five of all seven series. The H : h ratio also differed between days, the interaction χ^2 between days being also significant for at least four positions in four of the series.

In all but the first series, the heterogeneity χ^2 for days, with pooled positions, is greater than that for positions with pooled days. That is, the day to day differences in the H : h ratio are more pronounced than those due to the differences in position. Whether this has a biological interpretation or is a meaningless statistical accident of the data is not clear.

Since both occasion and position apparently interact with the height variable, their interplay with the species pattern, which also appears to interact with height, was next examined, as a preliminary to examining in greater detail their effect on the H : h ratio.

(*a*) *Species pattern and time*

That the trapping series has a 'main effect' in itself on the catch is obvious from the combined totals of Table 1. This effect on catch numbers could be due to differences in the mean weather conditions in each run of days, and so represent variations due to sampling chance from a time population, or it could be associated with the broader climatic pattern and represent samples from different, e.g. seasonal or annual, populations.

The data were therefore classified by species, year and season. For the last category, the July 1949 series was omitted and the three pairs grouped as early

and late season. The species groupings were the *Lc.*gp., *C.e.*, *C.v.*, and a combined figure for *L.s.*, *P.t-n* and *Cyn.* The total catch of the five pairs of traps over the five days was entered in the three-way table.

Table 5. *Analysis of variance by species, year and season*

Source	dF	Mean Square
Species	3	2 422 884
Year	2	615 178
Season	1	1 816 100
Species × year	6	565 419
Species × season	3	1 207 533
Year × season	2	474 295
Species × year × season	6	348 519

The season variance is very high, representing a standard deviation of nearly 1350 for the mean pooled catch of 415. Similarly, the mean square of the interaction of season with species, the interaction variance, is high. Were there in fact no season effect and consequently no season × species interaction, these two estimates would be independent estimates of the random variation. Their high value strongly suggests that they include rather more than 'error' variance, and that as estimates of error they are swollen by the inclusion of a considerable component due to their own effect. In comparison, the mean square for year, those for interaction of year with season and with species, and the second order interaction, do not differ much.

The second order interaction mean square (= S.D. 590) seems unduly high for an estimate of random variance. It may very well have a biological basis; the three years may have differed in their influence on the effect of season on relative species levels, producing a variance component of approximately the same order of magnitude as those for the years themselves, and those for the interplay of year with season and with species separately.

It is concluded tentatively that neither the differences in the three years between total catches nor the year differences in species pattern represent sufficiently serious discrepancies to invalidate pooling the results from the different years. The seasonal differences in catch level and pattern, on the other hand, are probably greater than the analysis indicates. The second series in 1950 was distinctly early (4 to 8 September). Its catch pattern corresponds more to that of the omitted July series than to those of the other two 'late season' series. Further, the May series, as will be shown elsewhere, represents a pattern which precedes the June pattern, and consists entirely of the early appearing *C.e.* species. For significance of the season effect over the generality of years, the comparative estimate of variances is that which includes possible interaction of the sample three years, i.e. the year by season mean square. Using this, the variance ratio, approximately 4 with only 1 and 2 degrees of freedom, is well below conventional significance, but is high enough to make untenable an assumption of there being no season effect.

The main effect, of a seasonal difference in catch level, is of little importance, as it may well relate only to the three years in question, but the evidence for it strengthens the suggestion in the analysis that the season × species interaction is a

true effect. If this interaction be accepted the problem of the effect of trap height becomes still more complicated—the impact of species pattern on the height response, suggested by the preliminary contingency test, will differ according to season!

(*b*) *Species pattern and position*

The high variability between the catches for the five positions, and the evidence of heterogeneous origin of a considerable proportion of the height differences, direct attention to the possible effect and inter-effects of this unavoidable variable. The July series, which yielded the best balanced distribution of species, was analysed in an attempt to evaluate critically the significance of what seems an ecologically improbable factor, namely, relative position of traps in uniform terrain.

The analysis was made using days 1 to 4 as replicates. The paired traps were regarded as one trap with entries at two levels, to equalize for possible height effect.

When the results are tabulated by position and according to species (*Lc.*gp., *C.e.*, and a pooled figure for the other species), the cell means show a definite regression on range for the 'other spp.' category; the two are independent for *C.e.*, while the *Lc.*gp. shows correlation for the lower values, but tends to independence with higher mean catches.

'Others'	Cell Mean	2	7	9½	12½	14
	Range	4	17	25	30	42
C.e.	Cell Mean	42	43	44	69	99
	Range	61	91	98	109	97
*Lc.*gp.	Cell Mean	5½	12	28	30	35
	Range	7	37	106	89	88

The *C.e.* and *Lc.*gp. results were therefore analysed separately (Table 6). As the *Lc.*gp. means and standard deviations are roughly proportional, instead of the means and variance, a logarithmic transformation (Log $\overline{n+1}$), was used for this

Table 6. *Analysis of variance of catches*

	C.e.		*L.c.* (logarithms of Catches)	
	dF	Mean Square	dF	Mean Square
Positions	4	2481	4	0·3394
Within positions	15	1877	15	0·3799

group. The 'within' group variance (which largely represents that due to days) is so great that it furnishes no useful estimate of random variance, against which to test the effect of position. The analysis, however, gives the following indirect evidence.

The mean trap catch of *C.e.* is 59; the two estimates of σ are 50 and 43. Thus the

scatter of results due to the combination of position and random differences, and freed of the day effect (indicated by the mean square for position) is actually greater than the scatter due to the day differences plus random variation (within position).

Assuming the variance of the means for position, (2481·4), to represent the sum of the effect of differences between these means due to position, (variance of means) and the variance of the position mean itself, (1877·4), then the mean catches per position have a variance of (2481-1877)·4 or 151, i.e. the basic standard deviation of the position means, shorn of the variability represented by their own standard errors, is approximately 12, instead of the theoretical zero for sampling from a common population.

Similarly with the *Lc*.gp., the mean logarithm of 0·9703 represents a geometric mean of 9·34 for the catches increased by 1. The (arithmetic) mean *Lc*. catch is 22. The σ estimates for the logs (of $n-1$) can be translated as a difference plus or minus of 3·8 times the geometric mean and 4·1 times, respectively. The scatter due to random differences plus position effect is thus in the same order of magnitude as that due to random plus day differences. It should be noted also that the day-induced deviation has been slightly over-estimated here, since the variance of the 'high mean' groups is lower than would be found in the complete regress of σ on x, assumed in the transformation to normality.

The species levels are widely different and obviously indicate different populations. A two-criteria analysis is thus not an entirely suitable method, but it is of interest that when the logarithms of the data are analysed thus, the main effect of position approaches significance, even when judged against the swollen estimate of error variance provided by day replicates (Table 7). The geometric mean ($n-1$) is 13·25. The error estimate of σ is $\pm 3{\cdot}08$ times, and the Position $\sigma \pm 5{\cdot}78$ times, the mean.

Table 7. *Analysis of variance by species and position*

	dF	Mean Square	F	F for P = 0·05
Species	2	4·5376		
Position	4	0·5804	2·43	2·58
Interaction	8	0·0828		
Error	45	0·2388		

The difficulty of interpreting the foregoing analyses lies in the lack of an estimate of the random variation of catches. Day to day differences are to be expected, because of weather and other day-associated factors which influence fly activity; these are additional to random variations, but because of the nature of the problem replications cannot be dissociated from them in the experimental design, without accepting the alternative of associating position differences with the replications.

The conclusions may be summarized thus. The time factor has a suggestive variance which probably has a seasonal component; season appears also to affect the differences between species levels. The position factor affects catch; this main effect, when examined separately for two species, suggested a rather higher level

of importance for *C.e.*, but the residual variance after separating the species and position components in a two-way analysis afforded no evidence of interaction.

Time and species factors in relation to height

Using the full set of seven series, the effects of time, species and height were examined by three-way analysis. The three numerically highest species, *Lc.*gp., *C.e.* and *C.v.*, and a pooled group of the remaining three species, were used. Within these criteria, the five days and positions were pooled for high and low traps.

(*c*) **Table 8.** *Species, series and height*

Sources	dF	Mean Square
Species	3	1 362 639
Series	6	334 234
Height	1	1125
Species × height	3	954
Series × height	6	11 787
Species × series	18	257 837
Species × series × height	18	5051

The analysis of variance is given in Table 8. The variance associated with height is here less than the second order interaction.

If it be assumed that there are not, in fact, two height populations, then the height means have a true variance of zero, and the mean square for height is an estimate of σ^2. In such case, as there can be no interaction with height, the considerable variance attributed to height on series is an accident of sampling, although the variance ratio, even with the largest estimate of σ^2 — the second order interaction — is 2·33, approaching the 5% level of significance (2·66). The alternative explanation is that height is a significant factor, the interaction of which with time is estimated by the almost significant mean square, but the main effect variance of which is, through accident of sampling, so underestimated that the height means must have varied less than random samples from one population would ordinarily do.

A point brought out by the analysis is that though the greater part of the variance attributed to time (series mean square) is due to the time difference in species pattern, a very considerable variance remains after all interaction components have been subtracted. This may be interpreted by saying that the time (seasonal?) differences are due to population depressions or increases acting on all species groups, as well as to differences in relative proportion of species.

(*d*) *Time, position and height*

For a final analysis the (untransformed) catch of total calliphorines for each individual trap on each trapping occasion was classified according to position, height and occasion (Table 9). The very high occasions variance here includes, of course, the day-to-day difference as well as the differences between series already examined.

The position main effect is, by this analysis, highly significant. If we regard

the occasions and positions as samples only of their populations, so as to make the findings applicable to time and position differences in general, the appropriate estimate of error variance for significance test is the random plus that attributed to effect of occasion on the position effect, i.e. the position × occasion mean square. The variance ratio of position to this is 5·6, whereas the value for even 1% level of significance is only 3·44. The position differences with occasion are also significant at the 1% level. The height interaction with occasion is significant at the 1% level, that with position at the 5% level. As in the previous analysis, the height main effect has a variance estimate less than the error estimate.

Table 9. *Occasion, position and height*

	dF	Mean Square
Occasions	36	18 958
Positions	4	4793
Height	1	194
Occasion × position	144	858
Occasion × height	36	1065
Position × height	4	1093
Occasion × position × height	144	328
Total	369	

The chief interest of this analysis lies in its confirmation of a significant difference in catch with traps in different positions. If the high and low traps of each pair (which, though differing in positions qualitatively, e.g. in relation to wind, were only 9 ft apart) are regarded as being in unit position, the position effect would appear from inspection to be due to differences between the low rather than the high traps. The range of 'high trap' means of total catch is 25·5 to 41·5, or 16; that for 'low trap' catch means 21 to 50·5, or 29·5. The standard error of differences between position means may be estimated by equating the mean squares to the components, following Snedecor (1946, p. 307). The second order interaction is our estimate of σ^2 (population):

Position mean square $=\sigma^2 p$ i.e. σ^2 (population) $+74\times\sigma^2$ (position mean)
$+2\times\sigma^2$ (occasion × position) $+37\times\sigma^2$ (height × position) $=4793$

Occasion × position mean square $=\sigma^2 p+2\times\sigma^2$ (occasion × position) $=858$

Height × position mean square $=\sigma^2 p+37\times\sigma^2$ (height × position) $=1093$

By substitution, $74\times\sigma^2$ (position mean) $=3170$, giving a standard error of the mean of $\sqrt{42{\cdot}8}$.

The S.E of a difference, $(\sqrt{2\times 42{\cdot}8})$ is approximately 9·3. Tippett (1931) gives range/S.E.$_{\text{diff.}}$ values of 2·5 and 2·8 respectively for 4 and 6 samples for 5% level of significance (p. 55, Table 11). For 'low trap' means, this ratio, with 5 samples, is over 3, that for high traps under 1·8. The significance of the position effect is thus due for the greater part to the discrepancies between the low level traps in the different positions.

DISCUSSION

The experiment was designed to answer the question: Does the catch alter appreciably if traps are raised 3 ft above grass level? Definite differences were

obtained, but there is no clear answer to the question of what factors influence occurrence of a catch difference with height difference. Of 175 comparisons, over three years, 85 were significantly different, 65 being significant at the 1% level; 59 were non-significant and 31 involved catches too low for reliable use of the χ^2 index.

Associated into groups, *i.e.* simultaneous catches over the 5 positions and runs of 5 days for a given position, the differences showed definite bias for each group, but the group homogeneity was by no means complete, some disturbing factor in each case causing differences either in relative size or in direction of the bias. The underlying group bias — the homogeneous element — varied irregularly from positive to negative in successive series of trappings.

The method of analysis of variance failed to assign an appreciable component to the height factor. The interaction components for height and occasion, and height and position were, however, significant (Table 9), and that for height and series (Table 8), approaching significance. In view of this, and of the definite significance of the height comparisons by χ^2 test, the failure to demonstrate a main effect of height is probably due to the uninformative distribution of the sample. The general answer to the originally posed question thus seems to be that raising the trap sometimes has no effect on the number of calliphorines caught, sometimes increases it and sometimes decreases it, the nature of the difference being apparently affected by, among other possible factors, a time-associated factor, presumably season. In addition, differences in extent, and even in direction of the height bias are produced, at any given season, by position of the trap pair, by a short interval time factor, presumably daily weather, and by the interaction of these two.

The experiment was not designed to provide an analysis of the causes of the heterogeneity of result, but the repetition of tests forced by this inherent inconsistency led to the accumulation of a considerable body of information, out of which certain possibilities suggest themselves; the preliminary examination of these, with a view to further exploration by experiment where indicated, is perhaps of more importance than the answer to the original problem. There appear to be three major sources of variability — species pattern, time, and trap position. These may directly affect the catch, or may influence the effect each other has on the catch.

The significant interaction of series on species reflects the differences, over the seasonal range, in the species pattern of the catches. The differences may be associated with season, or with chance differences between the weather conditions obtaining during the different spells of trapping; there is, however, a suggestive relation between the species pattern and the season (early or late). Either way, the result underlines the need for taking this time difference in species structure of the calliphorine population into account, when interpreting trapping results not obtained simultaneously.

The most interesting result of the experiment is probably the unexpected significance of position in a group of traps within reasonable distance of each other, relative to the assumed flight range of strong-flying diptera such as the blowflies.

There was no reason to suppose *a priori* that the five pairs of traps would not provide replicates from which to assess significance of any differences obtained with height, with days, and from interaction of these, yet a clearly significant position effect on the total catch was obtained. This effect was significantly influenced by the trapping occasion, *i.e.* a day interaction exists. One explanation of this interaction is that the direction of air movement, which frequently differs from day to day, may determine which traps of a group are first encountered by flies attracted from downwind.

With regard to the significance of the three factors in relation to the effect of height on catch:

(*a*) Species and height appear to interact, as indicated by the χ^2 contingency test for *L.c.*, *C.e.* and height, although the analysis of variance in Table 8 fails to reveal this.

(*b*) Interaction of both days and positions with height is suggested by the fact that the χ^2 measure of heterogeneity of height response in a given position over a run of five days, and for the different positions on any given day, is usually significantly greater than would ordinarily be obtained from random variation.

(*c*) Examination of the variance of position means reveals that the low traps have made the major contribution, *i.e.* the position × height interaction is due to the differences introduced by the low traps in the effect of position on catch.

Now, the *Lc.*gp. of flies showed a bias for low traps, *C.e.* a rather less marked bias for high. The position effect would thus appear to be due primarily to the *Lc.*gp. component of the calliphorine population. There may, however, be interaction of season with the response of *C.e.* to height — the May trappings, consisting entirely of *C.e.*, had a H : h ratio of 1 : 4. This probably accounts for the failure of the analysis in Table 7 to expose the species × position interaction.

The question of the effect of trap height is, after all, mainly of *ad hoc* importance. The laboriously expounded analysis of possible effects and inter-effects of other factors is given in some detail because it builds up, piece by piece, a mosaic of evidence for the existence of a distinct position effect, in addition to random error, resulting in a high degree of variability in simultaneous catches under conditions which may be regarded as exceptionally uniform.

Further work on the nature of this effect reveals that it is largely an intricate resultant of three variable contributory causes — a distinct, habitat-related, pattern of density distribution of the fly population, an almost kaleidoscopic movement pattern, unrelated to the underlying mosaic, of the individuals comprising the population, and thirdly a tendency to indeterminate aggregation of individuals, possibly at the protoco-operative level, but occasionally at least due to an identifiable ephemeral cause. The evidence for these has gradually accumulated as incidental to the general study of the physical and community relationships of the blowfly group, and cannot satisfactorily be presented in anticipation of the main ecological account; it is hoped to submit this in later papers.

ACKNOWLEDGMENTS

I am much indebted to my colleague, Mr J. Donnelly, who has shared the labour of collation and mathematical handling of the trap records, and to Mr J. G. Skellam, of the Nature Conservancy, for reading the manuscript and making helpful criticism of the statistical treatment of the data. He has recalculated the significance of the differences in Table 1, using the log $n+1$ transformation, but obtained much the same result as that given by the raw data.

SUMMARY

1. An experiment is described which compared the effect of having fly traps at grass-tips level and raised 3 ft. Five pairs of carrion-baited traps were distributed in a rough circle of less than 100 yd diameter, in ecologically uniform terrain. The sequence of tests extended over three years.

2. Differences in catch varied in amount and direction between successive tests. Analysis of the differences suggests that the catch-response to trap-height is affected both by the differences between days and by season. These affect the species distribution of the flies caught, and this in turn affects the relative catch level of high and low traps.

3. The position of a pair of traps in relation to replicate pairs influenced the catch-level for the pair; this 'position effect' in an apparently uniform environment varied between days and for species. It appears to be due largely to the *Lucilia* component, but indirect evidence is adduced for a similar effect with *Calliphora erythrocephala*, the major component of the population. A relation between species, position and height is inferred.

4. Possible causes of the definite grouping of blowfly populations are briefly outlined.

REFERENCES

Snedecor, G. W. (1946). *Statistical Methods.* Ames, Iowa.
Tippett, L. H. C. (1931). *The Methods of Statistics.* London.

SEGREGATION OF SPECIES OF THE ANT GENUS *MYRMICA*

By M. V. BRIAN

Zoology Department, Glasgow University, and the Nature Conservancy, Furzebrook Research Station

(With 1 Figure in the Text)

INTRODUCTION

This is a study of the ecological relations between two congeneric species living in natural conditions. The genus *Myrmica* is widely distributed in temperate regions of the earth, and all species are similar in form. Two of them, *M. rubra* L. and *M. scabrinodis* Nyl. (henceforth symbolized *r* and *s* respectively) occur together in an area of west Scotland between Loch Lomond and the Firth of Clyde. That they are quite distinct species is not in doubt, for no intermediate forms have been recorded although their geographical ranges overlap almost completely. The reproductive barrier appears to be a psychological one for the males of *s* attempt to copulate with the *r* females but are repulsed; these can evidently distinguish between males of the two species. It is of interest to note that *s* comes later to the (same) nuptial grounds; this is not relevant to the present problem as there is no danger of crossing, but was very relevant to one involving two forms of the species *r* (Brian & Brian 1955).

It is not therefore with the mechanism of genetic isolation that this study is concerned, but with the means by which such species, which by reason of their similarity in form and behaviour would be expected (Darwin 1859) to have similar requirements, manage to live together in the same habitat, when this is defined superficially in terms of edaphic and vegetational characteristics. For it has been shown theoretically by a great many workers using either logical or mathematical arguments that if two species compete freely (that is with otherwise unrestricted population growth) for only one essential resource that is limited (and this must apply in practice to all resources) both cannot survive together indefinitely. But it is at once obvious that the means of co-existence must in practice be numerous (which does not in the least detract from the value of the theory) and one of the principal of these is environmental instability (at any rate today; perhaps before human dominance in the ecosystems this was different). In illustration of this, one may recall that these two species occur together in seres without any sign of habitat segregation, although this appears in older plagioclimaxes (Brian & Brian 1951, Brian 1952*b*). The actual rate of segregation varies very much with the method of colonization, being much quicker (say 2 years instead of over 5) if mature colonies have access to the area (as an example of this consider the turf banks mentioned in Brian 1952*b*).

A few general points may be considered here, so that later remarks are clear. All animals require certain basic resources (food, nest-site, drinking site and so on) which they obtain under various different conditions of climate and topography which may be called modifying factors. Only the spatial variation of these need be considered for the moment; by varying in their intensity, such factors create environmental heterogeneity of a nature that predisposes species to segregate by one or other of the known methods. These fall broadly into two groups: the first consists of the selection by instinctive behaviour of totally different habitats (that is resources and modifying factors combined) and is a method expected of taxonomically distant forms; the second, an interactive process, ensues when this selective segregation is imperfect and the species choose habitats that overlap, or more precisely when they attempt to share certain resources. The first is referred to as the selective, and the latter as the interactive or competitive method.

This latter process is now realized to be extremely complex, consisting of blends in various degrees of individual and group behaviours with population turnover. Of a purely behavioural nature is the segregation that is learned, either through appreciating that resources are less easily tapped where the other species lives, or through direct appreciation of the unpleasant nature of the other species. These processes cause segregation without any population change whatsoever, merely by translocation of units. Where translocation is impossible segregation must depend on population turnover, and in its simplest (theoretical) case, it may develop whenever one species is more efficient in a habitat than another, perhaps because it can find and use vacant unit resources more easily and quickly than the other. This process has been termed 'exploitation' (Crombie 1945, 1947, Park 1954) but is referred to as 'natural selection' by Elton & Miller (1954). It may be accelerated by interference between the species which consists in damaging the other species directly or preventing its access to or damaging its resources, so that its biotic potential is reduced.

It may be noted that the purely learned behavioural segregation is divisible in a like manner into that generated by species differences in exploitation (learning to avoid areas that are more effectively used by another species) and that generated by interference (learning the unpleasant nature of the individual). In fact, in general, interaction may be sub-divided into exploitation and interference and it may lead to behavioural segregation in the appropriate environment if translocation of population is possible, but if not, then it must await the processes of population turnover.

GENERAL HABITAT DIFFERENCES

The so-called preference of *s* for drier, more exposed habitats than *r* has frequently been recorded in the myrmecological literature. This raises two points that must be immediately clarified. The first is that in an earlier paper (Brian 1952*b*) a variety of evidence both experimental and observational was produced which showed that (at any rate in the Clyde area of Britain) this habitat difference

was due to a competitive process. Habitat selection by both species, which lay with the foundress queens and nomadic spring colonies was based on the spring character of the terrain, and took no account of the total annual character of it. At this time of year the warmest places were chosen, and they were invariably wet but not waterlogged. Interspecies conflict had an almost clear-cut success order. This competition for warm sites to live in is understandable in animals of tropical derivation (with similar temperature-growth relations) living at a northerly latitude where cloud obscures the sun for about 70% of daylight hours. Moreover vegetation adds a further screen to this, letting through radiation in a way that is partly species specific and partly height controlled. It is important in what follows to realize that grass only 25 to 30 cm high excludes enough heat to reduce materially the rate of brood maturation in colonies of *r*. (Brian & Brian 1951.)

The second point concerns the confusion between soil water content and temperature and their interaction—perhaps better called an intuitive appreciation of causal relationships (derivative even from human habitat selection behaviour). Soil moisture content is largely dependent on drainage but is also affected by evaporation which may be accelerated by wind or sunshine. Hence, drainage being equal, those areas that receive insolation will be drier as well as warmer than those that do not. Further, soil moisture also affects the soil temperature in various ways (Richards, Hagan & McCalla 1952); wet soil is a better conductor than dry and prevents the accumulation of heat on the surface, it has a higher specific heat, the water evaporates and absorbs heat, the surface may reflect more radiation, a screen of water vapour may be formed just over the soil which reduces radiation penetration (in both directions but less away owing to the lower temperature of the source). All these facts combine to make the surface layers of a moist soil cooler than those of a dry one. There is an additional factor that links drainage-moisture with insolation-moisture, and that is that the best drainage is on slopes especially banks; and when these face south, they have a better aspect, and absorb more energy per unit area thus drying out and warming up in two ways at once. Thus the situation is complicated and there is good reason at the present stage for retaining the 'warm-dry' intuitive association as a habitat description.

Besides general reference to the habitat differences of the two species (in faunistic lists and general books on ants) a number of surveys of ant distribution have been made in different parts of Europe. In so far as they concern *Myrmica* they are unfortunately not always comparable, for sometimes the presence of a forager was enough for a record, and sometimes the author sought the nests. Now although workers of this genus never wander far from their nests they may nevertheless penetrate into quite different vegetation. The potential foraging microclimate has a much wider range than the potential nesting climate; workers can run actively in tall vegetation that is much too cool for the growth of brood. This distinction between foraging and nesting areas is of wide ecological importance.

The relevant parts of these works may be briefly reviewed. Skwarra (1929) who was concerned with the ant fauna of moorland on the southern shores of the Baltic Sea found *r* (called *M. ruginodis* Nyl.), but she noted that *s* avoided dense wood-

land especially if damp. Gösswald (1932) found that in Bavaria *r* was most abundant amongst open conifers on a sandy soil and he considered it xerophil and stenotopic, a conclusion based on its distribution; *s* was found in even drier stonier ground with only sparse coniferous cover, and it even extended into the dry areas inhabited by typically Mediterranean species. Jacobson (1939) noted that in the east Baltic states *r* occurred in woodland rather than in dry open places and it is called 'the common wood ant' in Russia, whereas *s* is the ant of open landscapes. Diver (1940) found in southern England that *r* 'prefers the shade effects of taller vegetation, and damp places, whilst *s* prefers shorter vegetation and on the whole drier places'. Westhoff & Westhoff-de Joncheere (1942) pointed out that in Holland *r* alone penetrated dense woodland, *s* being characteristically in open dry birch woods. Thus in these well separated areas of Europe there is general agreement between authors that *s* tends to live in drier warmer habitats than *r*, but that a variable overlap occurs.

To this list can be added a general statement about their distribution in western Scotland, based, as were all the above, on a subjective estimation of the environment. On this basis *r* was eurytopic and ranged from almost bare lichen covered dry patches in heather moor, right into shady damp woodland, whilst *s* ranged from the first up to but not including woodland, in which it was only found in large glades. The actual habitat range of *s* was thus less than that of *r* through a failure to penetrate as far towards the damper, shadier end of the scale. It has been pointed out before (Brian & Brian 1951) that in a pine plantation the size of the nests of *r* increases with the glade size, which was measured as hours of potential sunshine, and *s* was found only in glades larger than any of those considered.

However, even *r* could not be considered the common wood ant as in Russia. In general it seems possible that in southern England, Holland and Germany, the Baltic area, and Russia the distribution of the pair of species is displaced compared to western Scotland towards the woodland type of habitat, which may perhaps be accounted for by the sunnier drier climates of these places. The same geographical shift in habitats occurs in grasshoppers (Richards & Waloff 1954) for most of the British species live in open habitats in this country and often in woodland or marsh on the continent. In the sunnier climates the range of variation in soil microclimate would be expected to be increased by an extension at the hot end, and a given microclimate would be expected to occur under less proportionate penetration of insolation. The ant fauna in general supports this prediction, for whereas *Formica fusca* L*. and *Leptothorax acervorum* Fab. live in lichen covered places in Scotland even in the neighbourhood of the two *Myrmica* species (Brian 1952*b*) this type of vegetation is associated with the Mediterranean species in Bavaria (*Tetramorium caespitum* L., *Solenopsis fugax* Lats.). At the other end of the scale whereas *r* alone ranges into the shade of woodland in western Scotland, in Bavaria two additional species, *Myrmica laevinodis* Nyl. and *Lasius niger* L., penetrate into areas of apparently even lower proportional penetration of insolation.

* This species is now known to be *F. lemani* Bondroit, a form very similar to *F. fusca* L. (see Yarrow 1954), but to retain continuity with past publications it will still be referred to as *F. fusca* L.

However, the stability of the habitat certainly plays an influential role as well as the insolation for only where a certain permanence exists can populations build up to a level where competitive actions affect distribution. This factor may account for the disagreement between the Westhoffs and Gösswald; for the former regard *r* as eurytopic, but they were studying a young community rather than what may well have been a stable old one. Until the essential microclimatic features are measured quantitatively, and age and mechanical stability assessed, fruitful comparison of distributions in different regions will be impossible. The present comparison has been enough to show that many interesting results should follow.

In the New World too, the differences in distribution of the species of *Myrmica* appear to be affected by soil moisture and warmth (Weber 1948). Perhaps *M. schenki emeryana* is equivalent to *r* and *M. sabuleti americana* to *s*.

EXAMPLES OF HABITAT PARTITION

It is with the distribution of nests in small areas of the order of 100 sq. m that this study is concerned. It has already been shown (Brian 1952*b*) that in a plagioclimax in a felled woodland subsere *s* tended to be more frequent in the elevated warm dry stumps than in between, and that on these stumps, which were of about 1 sq. m in area, they occupied on the whole more easterly positions than *r*. *Formica fusca*, the dominant species, occupied the southern aspect (cf. *Formica truncorum* F. in Norway—Elton 1932), so that in very heterogeneous areas that offered a finely patterned mosaic of variable quality nest site it was possible for the two species (as well as *F. fusca* and *L. acervorum*) to co-exist within less than 1 m and yet develop a partial partition of nesting-habitat. In other words, they were only living in the same type of area when this was defined in the most general terms as a biotic plagioclimax. This biotic plagioclimax was in many respects perhaps unusually heterogeneous. Four examples of less finely patterned mosaics will be given, taken from acidic grassland after (as far as historical research shows) at least 50 years of freedom from interference. The two species that cannot build small mounds of soil (*F. fusca* and *L. acervorum*) are necessarily rare or absent so that attention can be concentrated entirely on the Myrmicae.

(*a*) *A turf-covered scree*

This was on the side of Ben Bowie (313 m) and formed from its basalt cap. A cliff of 8 m had been left after the stone had fallen from a scree 11 m long, sloping 1 in 4 with a southerly aspect and having the largest stones at the bottom. As most is now covered with turf it must be presumed that either the fall was sudden and transient or that it continues slowly. The turf was principally of *Festuca* spp. with *Rumex acetosella* L. and *Polytrichum* spp. (Fig. 1, type *a*) on the shallower soil 0-10 cm deep; on deeper soil (10-15 cm) surrounding this it was principally of the above with in addition an admixture of *Agrostis tenuis* Sibth., *Galium hercynicum* Weigel and *Potentilla erecta* (L.) Rausch. (Fig. 1, type *b*). At the foot of the scree yet another type of vegetation could be distinguished composed of sparse dwarf

Pteridium aquilinum and the grasses *Agrostis tenuis* and *Holcus lanatus* L. on soil from 15-20 cm deep (Fig. 1, type *c*). An even deeper soil (80-100 cm) occurred on the east side in which *Pteridium aquilinum* (L.) Kuhn and *Urtica dioica* L. were characteristic (Fig. 1, type *d*); this soil was so deep that rabbits (*Oryctolagus cuniculus*) burrowed, and the nettles lived mainly in their excavated debris. The cliff itself had in the cracks *Festuca ovina* L., *Polytrichum* spp. and *Teucrium scorodonia* L. In addition to the rabbits, sheep grazed sporadically.

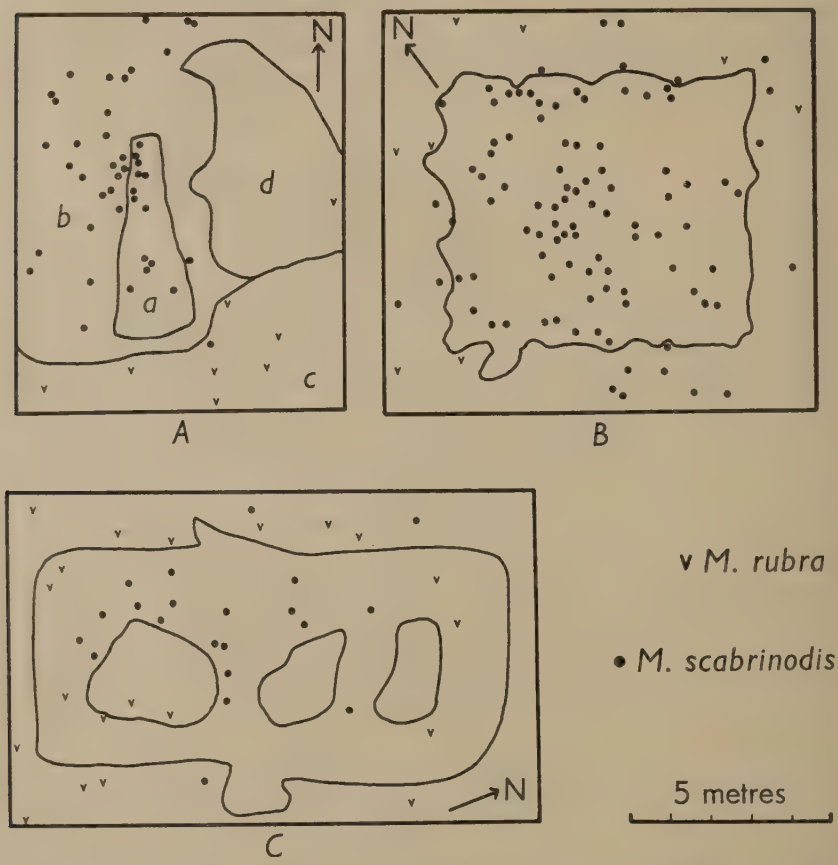


Fig. 1. Distribution map of nests of *Myrmica rubra* and *M. scabrinodis*. *A*, a mountain scree, with zones *a* to *d* of increasing soil depth and characteristic vegetation (described in the text); *B*, a patch of heath in acidic grassland, with the heath vegetation outlined; *C*, the grass covered remains of an old ruin, with a contour of about 0·5 m plotted to indicate the position of the banks, the three central depressions being traces of rooms.

The ant distribution is evident from Fig. 1*A*. In an area of 177 sq. m, fifty-seven nests (strictly surface mounds; it is possible that the number of nests was less than this as a single colony may occasionally build more than one annex above the soil

surface) were discovered after a careful search under ideal conditions of moist, warm surface soil with cold underlayers. Of these nests, forty-three were *s*, eight were *r*, and six were *L. acervorum*. Five of the last were in cracks in the stones, and one under a stone; both these and all but one of the *s* nests were in vegetation of types *a* and *b*, the *s* principally at the top of the scree in the shallow turf over small stones, where a density of 4·2 nests per sq. m was recorded. By contrast the *r* were represented by one nest in type *d* vegetation, and seven in type *c* along the lower margin of the scree; the nests were placed either against or under the comparatively large stones of this area; one *s* nest was in this type too.

Such a distribution is felt intuitively to be non-random, for it is possible to envelop all the *r* nests in a non-inflecting curve which includes only one *s* nest. Even so, the following statistical test was applied. It depends on the theory that the nearest *n* nests to a point selected randomly should if the two sorts are both distributed randomly contain *k* ($k = 0, 1, 2 \ldots n$) nests of type *s* with a probability given by the binomial theorem that may be symbolized $b\ (k; n, p,)$ where p and q, the elementary probabilities ($p + q = 1$) are the proportions of *s* and *r* respectively in the total number of nests. Thus choosing *n* to be 5, since $p = 43/51 = 0{\cdot}843$ and $q = 0{\cdot}157$ it would be expected that after 53 tests (each based on a point selected with a table of random numbers) there would be 0, 1, 2, . . . 5 *s* in 0, 0, 1, 8, 21 and 23 cases respectively whereas in fact 0, 14, 4, 7, 5 and 23 were obtained in the trials. Hence far more singles and far less fours were recorded except at the boundary between the *s* and *r* areas, which accounts for the intermediates. It was in fact the single *s* nest in the *r* area that prevented the occurrence of zero records. Using the χ^2 test it can be shown that the observed result is improbable by chance ($P < 0{\cdot}01$) and hence the case for a non-random distribution is very strong.

The interpretation of this must not be pushed too far however, for if the nests of each species were aggregated but distributed independently of the other species, the chance of a non-overlap of these aggregates might be quite high, certainly higher than if the nests of both were randomly distributed, and a significant χ^2 would result. Hence this result may only mean that intraspecies nest-aggregation occurred, not that there existed some sort of avoidance mechanism. Nevertheless it has been shown elsewhere (Brian 1952*a*, *b*) that such a mechanism exists, and the proximity of the populations make it reasonable to suppose that it has in fact played a part in the generation of this state.

Six standard chemical tests were done on five samples of the soil from each species region*; the means of these are given in Table 1. They show that compared with good agricultural soil that of the slope was very acid, with high organic matter, and that whereas the potassium is moderate, perhaps owing to the basalt, the phosphorus was deficient. The only significant differences are the small ones of pH ($0{\cdot}05 > P > 0{\cdot}01$) that of the shallow soil in close contact with the basalt being slightly less acid. The moisture is not different, which is not surprising as the

* For the analyses I am indebted to Dr Whittles, West of Scotland Agricultural College, Auchencruive.

samples were taken in September after the summer period of rainfall when the ground is normally saturated. In the dry season of May and June there is no doubt that the *s* area becomes far drier than the *r* area, for the turf becomes quite brown.

Hence the usual partition of the habitat is observed. *s* living in shallow soil that is well drained, with short vegetation that is liable to suffer severely in drought (no doubt for most of the year the soil is moist enough for them to get the benefit of the surface warmth), *r* living in deeper soil with taller vegetation that is less affected by drought and receiving less benefit from insolation. Thus the conditions for the replacement of *r* by *s* exist in the former zone (Brian 1952*a*, *b*) and the evidence is strongly in favour of the view that there is here a segregation through interaction.

Table 1. *Chemical characteristics of the scree soil of Ben Bowie in the area populated by Myrmica scabrinodis and in that populated by M. rubra; each figure is the mean of five samples*

	Area populated by *M. scabrinodis*	Area populated by *M. rubra*
pH*	4·44	4·17
% moisture	7·7	7·3
% loss on ignition	37	28
% K_2O	0·021	0·023
% P_2O_5	0·0054	0·0044

* a difference with a probability between 0·05 and 0·01.

(*b*) *A heath area in grassland*

This is a rectangle of heath 10 by 11 m surrounded by acidic grassland. The heath vegetation is itself dual, consisting of a mosiac of shrubs of *Calluna vulgaris* (L.) Hull, *Erica cinerea* L., and *E. tetralix* L. about 8 to 30 cm high which covered about 75%, and of short herbs and grasses (*Festuca* sp.) sometimes only 2 to 3 cm high, with a large admixture of moss (*Hypnum* sp.) covering the rest. The heath is surrounded by acidic grassland with predominant *Agrostis tenuis* (10–15 cm high), *Festuca* spp., *Galium hercynicum* and *Potentilla erecta*, lightly grazed by rabbits and sheep (during the summer) but not enough to prevent flowering. Apart from a few isolated bushes of *Calluna vulgaris* this was typical grassland for at least 20 m all round the heath area.

The ant population in the rectangle (Fig. 1*B*) consists of pure *s*, seventy-seven nests in all located without exception in the short mossy zones and giving a gross density in the heath area of 0·70 nests per sq. m. An area of the grassland forming a border of 2·5 m width and 130 sq. m area contained twenty *s* and eight *r* nests. The density of both together is thus 0·22 per sq. m, about a third of that in the heath rectangle. This differentiation between a central dense *s* population in short vegetation and a sparse mixed population in taller vegetation around seems intuitively improbable by chance and statistical tests have not been applied.

It has not been possible to account precisely for this curious patch of heath. Historical investigations have shown that it was part of a small farm (croft) which disappeared between the first Ordnance Survey in 1860 and 1880 (a date recalled

by an old inhabitant). The foundations of the farm buildings were traced, as they carried an identical type of vegetation, but nothing equivalent was found in the rectangle in question. However, its shape makes it highly probable that it was either a building without foundations (of wood for example) or a cattle enclosure. The soil analyses throw further light on this.

Table 2. *Chemical characteristics of the rectangular patch of heath surrounded by acidic grassland; each figure is the mean of five samples*

	Heath	Grassland
pH*	4·50	4·74
% moisture	1·6	1·3
% loss on ignition*	6·2	5·5
% K_2O	0·0094	0·0112
% P_2O_5	0·0014	0·0014

* a difference with a probability between 0·05 and 0·01.

The soil in the area as a whole was a buff coloured sandy podsol overlying glacial drift and quite acid (Table 2), very deficient in phosphorus (less than the scree soil) with moderate potassium (although only half as much as on the scree) and little organic matter (about one-fifth that on the scree) whilst the moisture at the time of the sample was low. Slight but significant ($0{\cdot}05 > P > 0{\cdot}01$) differences between heath and the surround concerned the pH (lower inside) the organic matter (higher inside), all of which differences could be derived from, rather than caused by, the vegetational difference. The soil structure and profile were identical in both areas.

Thus the general evidence favours the idea that this rectangle was covered by a shed in which implements and straw rather than beasts, which would have left more phosphorus, were kept. It might have been a dry stone or wooden shed but not a mortared building, since there were no foundations and no excess of lime. On its removal heather which is the natural shrub in prisere growth would have colonized the bare soil surface, and under only light conditions of grazing maintained itself distinct from the surrounding grassland, a direct product no doubt of the agricultural practice of the crofter. During the period of agricultural depression the maps indicate an extensive re-invasion of the lowland grass by heath so that seed would have been available.

Hence once again, the conditions appear right for the interactive partition of the heterogeneous area: a central area of high soil insolation with a high density of *s* (although this time not conspicuously prone to severe drought effects) surrounded by an area of taller vegetation with a low density mixed population. Where the competitive pressure is likely to be highest is the pure population. It will be recalled that severe soil dessication although likely to assist replacement of *r* by *s* was not essential (Brian 1952*a*, *b*). Whereas in the first example (the mountain scree) the partition is based on a geological-historical feature, in this case it is based on a human-historical feature.

The condition of low density in the grassland is worth further consideration. There is no doubt that as a nesting site it is inferior, owing to the tall grass. The

best loci in it are the mounds made by moles and then left undisturbed so that a crust of rain-beaten soil forms, below which the ants nest; even so, these have been shown to be inferior to sites under stones (Brian & Brian 1951). There is no reason to suppose that grassland is a better foraging area than heather, for the latter contains abundant small insects. Thus the grass fringe with low ant density may be regarded as one of inferior nesting value, in which the sites are scattered and transient (mole hills). If these were colonized by young queens which had produced enough workers by the time the hill degenerated to enable them to make their own hill and survive in the encroaching vegetation, it is possible that the population of the grassland could be slowly built up to a self-regulated level. On the other hand it is certain that the mature colonies would move into the new hills and by interference prevent the young queens from producing more. Population will thus be likely to be self-regulated at a far lower density, which will be a function of nest-site density and the distance over which workers can move their colonies. Species segregation even of a mosaic type (like that of plagioclimax grassland—Brian 1952*b*) would not be expected to follow saturation, owing to the constant flux.

(*c*) *A buried ruin*

Before 1842 this was a house, but afterwards it was largely pulled down and used as a fold for sheep. It had, however, been in complete disuse for at least 50 years before this study, and it is now no more than a series of grass-covered mounds and ridges never rising more than 0·5 m above the general ground level. The grass and moss on the ridges is closely cropped by rabbits and sheep but in the gullies between, which represent the old rooms, it is taller and the plants *Juncus conglomeratus* L. and *Urtica dioica* occur.

The wall-top sites although dry and warm are not monopolized by *s* as might be expected, but a central mass of eighteen nests can be circumscribed by a line which includes no *r* nests, and outside these were twenty *r* and only three *s* (Fig. 1C). The total area surveyed covers 238 sq. m and the central area of pure *s* 54 sq. m, giving a density within of 0·33 per sq. m and without of 0·11 per sq. m. Thus although these densities are gross and include areas of tall grass that are probably uninhabitable, there exists a situation similar to the preceding: a central core of higher density pure *s*, surrounded by a fringe of low density mixed *s* and *r*. In this case, however, the *s* area is not clearly related to any conspicuous vegetational feature, and it is more important to apply the statistical test used with the scree data. When this is done, it is found that the distribution expected if the nests of both species were randomly distributed and independent of each other is very closely approached in practice, and a χ^2 test after 100 sample points gives a probability between 0·5 and 0·3.

This is then the best solution to what otherwise would have been a puzzling problem, for not only is there no difference in the vegetation in the *s* area, but there are no differences in the soil either. Combining all samples and treating the area as a whole, the pH was much higher than in the other localities averaging 7·5, owing no doubt to the lime in the mortar of the old building; the organic

matter at 6·7% was low, the potash was normal at 11·4 units, and the phosphate was very high at 13·3 units, owing no doubt like the high pH to earlier human occupation.

The problem here is why have the *s* not occupied all the ridges and the *r* all the dips? This is unanswerable and might be referred to the time for which the area had been suitable for ants. Suitability would no doubt start at the bottom of the walls and the tops would only become available much later; it is likely then that a long period of *r* colonization of the wall bases, under stones that lay about in the long grass and other herbs, preceded the approach of conditions suitable for *s*. This, combined with the fact that there are no ant sites nearer than 100 m. might well account for their weak establishment.

ADAPTIVE DIFFERENCES

As *s* have been shown to replace *r* in warmer drier loci that are for most of the year in most years the best nesting sites, and certainly the best at the time of year that they are chosen (excessive drought is rare in western Scotland) the question naturally arises: 'What prevents them replacing *r* entirely in the region studied?' As no active interference of *r* with *s* has ever been seen the answer would be expected to lie in a difference in adaptation which gives *r* an advantage over the other in certain habitats, and perhaps even allows it to enter areas that are useless to *s* —the cooler, moister sites in longer vegetation. It is not necessary that *r* be attracted towards these, in fact as already stated both appear to be attracted towards the same nest-site and *r* would doubtless occupy the whole range of habitat type were it not for *s* and the other species. A study has therefore been directed towards finding adaptive differences which would account for the inability of *s* to occupy the whole range of habitat type.

A difference in temperature relations was first sought, but it was found that neither larval growth-rate, nor pupal maturation-rate, both important aspects of colony growth, were different; indeed if anything *s* have the advantage of slightly quicker maturation at lower temperatures. Crude survival of high and low temperatures were not tested as the animals are perfectly able to avoid extremes. Nor has any difference in worker activity been noticed, although this is less easy to measure particularly under realistic working conditions as it is complicated by social and extrasocial influences. Thus as far as physiological temperature relations are concerned no species differential of the sort required exists.

A species differential exists as regards resistance to low humidity but is not relevant to the present problem; Gösswald (1938, 1941) showed that *s* was more tolerant of and more resistant to low atmospheric humidities. The relevant question: 'Does *s* suffer more than *r* at high humidities?' appears to be satisfactorily answered by the fact that both species spend most of their life in air saturated with water vapour and clearly suffer no ill-effects.

After this some aspects of behaviour were investigated. Year by year recording of nest positions on a permanent quadrat had shown that a greater proportion of *r* nests moved, but the result was not statistically significant. An experiment was

therefore designed to test this: ten nests of each of the two species were shaded by means of brushwood screens during sunny weather in May. Within one week all had vacated their sites. Thus both *r* and *s* move readily in response to shading and no species differential was apparent. Since *r* live in longer vegetation on the whole they are likely to move more often than *s* for ecological reasons rather than intrinsic differences in reaction.

The species difference in vertical foraging distribution that has been described elsewhere (Brian 1955) was the first positive result. *S* concentrated on soil surface search far more than *r* which climbed herbs and grasses to a considerable extent, as well as searching the ground layer. The shape of *s* and its manner of progression clearly adapt it for the crawling insinuating type of movement that is necessary when in grassy vegetation near the soil surface. It has shorter legs than *r*, and it frequently folds its antennae against its head; thus even the sharply bent scape of *s* (one of the characters used in taxonomy to differentiate it from *r*) may have adaptive significance through facilitating this folding action. On the other hand *r* has longer legs, and is able to run quickly over leaves especially in mixed grassland with horizontal leaves of *Potentilla erecta* and *Galium hercynicum*. The significance of this to the present problem is that during the day in sunny weather *r* moves in the warmest stratum between the soil surface and the tops of the herbs, and is able as well to benefit directly from the solar radiation. This then is a feature that should assist the foragers of *r* to penetrate into longer herbs more than about 5 cm high than *s*. It must also be an advantage in soil that is liable to become waterlogged and may account for the common records of *r* living in tussocks in bogs (like *Formica picea* Nyl.).

It was implicitly assumed (Brian 1955) that these differences were due to differences in instinctive feeding-zone selection, for no interspecies aggression was seen except on small permanent fixed food sites which were frequently monopolized by one or other of the species. It was pointed out that success in this monopoly depended less on fighting ability than on finding and covering the food—superior powers of exploitation followed by interference of the type involving prevention of access to resources. In view of the fact that this is effective and that ants actively avoid interspecies contacts in the field, one cannot exclude the possibility that the feeding stratification owed something to learned avoidance on the part of the foragers (that in certain areas they were more likely to avoid contact with the other species). An explanation of some cases of intercolonial distribution of *r* on these lines has already been advanced (Brian 1955).

Nest architecture was next studied. Both species excavate galleries in the soil and build small mounds of vegetable debris and soil between the stems of herbs. In a series of measurements of the mounds in typical acidic grassland from which cattle and sheep had been temporarily removed, so that free scope for building in a rising grassy herbage existed, no species differences were detected in size and shape. The mean height of sixteen *r* mounds was 6·0 cm in herbs of average leaf height 8·6 cm, and the mean height of ten *s* mounds was 5·8 cm in herbs of average leaf height 6·9 cm (note the lesser value here). The difference of 0·2 cm was not

statistically significant. Nor was any difference in basal width discovered, the mean of all twenty-seven being 5·6 cm (if the basal section was elliptical rather than circular the lengths of the two axes were averaged). Some of the nests were no wider at the bottom than at the top, and looked more like columns than mounds. Thus there is no reason to suppose that *r*, as might have been the case, are better at building into herbs than *s*. The difference lies rather in the internal architectural style, the main features of which have already been described (Brian 1952*a*). Under glass plates covered by slates it is possible to observe that *s* fill in with soil any air-spaces between the soil surface and the glass that exceed 5 mm, so that on completion their cells are 3 to 5 mm from floor to ceiling. In large air-spaces they may construct several tiers of cells, which are usually connected by so many holes and passages that the 'layer' formation is obscured. The whole structure is an intricate spongework of plastered mud so applied that their cells are often large and irregular with floor to ceiling distances of over 9 mm. They are much more influenced by natural features such as sticks, worm-casts, etc. Against the side of large stones, both species build more regularly so that the layer formation is usually clear; again it is possible to note that the modal distance between floors is 5 mm with *s* and 9 mm with *r*.

In the laboratory, it has not always been possible to induce building, even in strong vertical thermal gradients. However, occasional success attended the use of crystallizing dishes with straws stuck vertically at 10 mm intervals in a thin layer of wax on the bottom; sieved moist soil was added and kept moist with an atomizing spray. Several times different colonies of *r* cleared the soil from the bottom and built a cylindrical screen not against the glass side, but going from straw to straw, about 10 mm from the glass side, and reaching from floor to roof of the vessel. This screen was built against the light side and was later covered over to form a tent. The *s* never did this; rather they excavated in the soil and formed a foam-like structure that was self-stable and did not depend like that of *r* on the straws for support. The bearing of this on the problem under consideration is twofold. The greater skill that *r* show in the use of natural features as walls and girders, should be of great advantage in fairly tall vegetation that is liable to change from month to month, and is not subject to the trampling action of small mammals. At the other end of the heat-water scale the *s* type of nest will have more permanence, and be better able to resist dessication and the light trampling action of small grazing mammals that are responsible for maintaining the short character of the herbage without which the ants could not survive.

Thus the evidence shows that both species are adapted to the habitat type in which they preponderate (and this has frequently been shown for other animals; for ants one may cite Talbot 1934) and good reasons exist which prevent *r* from being eliminated by competition with *s*. It has proved to have substantial adaptations to a life in longer vegetation: a shape adapted to moving quickly and freely in the warmest zone during sunshine, and a method of building which is economical of material and likely to confer plasticity in the face of a growing vegetation that may become waterlogged. These enable it to obtain access to insolation even

though it lives in long herbs, and to exploit the rich food reserves that occur there (Collembola, dipterous larvae, etc.). It is no doubt these features that enable it to live in the otherwise antless habitat of old Callunetum, for the 'leggy' plants keep the soil very cold indeed in summer, but provide in their loose mossy centres good building sites.

DISCUSSION

The facts that have been established in this and four previous papers (Brian & Brian 1951, Brian 1952*a* and *b*, 1955), and that are relevant to the ecology of congeneric species may now be brought together. Two species of *Myrmica* occur in the area studied, both 'together' and separately—for example in woodland only *r* is found. They occur together in seres, and show no segregation (heather and felled woodland subsere), but in areas where change is slow or non-existent the habitat is divided between the species so that the apparent co-existence is really due to the mosaic distribution of modifying factors, chiefly the degree of soil warmth and moisture. In other words, large scale co-existence is small scale segregation. In these areas *s* lives in short turf, and *r* in longer grass-herb vegetation.

Some of the causes of this segregation have been analysed. First, several lines of evidence have indicated that it is not based on strictly differential habitat selection (selective segregation), indeed both species appear to seek the same warm well-drained sites in which to live; but rather that it results from competition (interactive segregation). Some progress has also been made in understanding how this works. In the first place sufficient adaptive differences have been found for segregation to develop through exploitation alone. These are: the workers of *s* have a form that fits them for crawling through dense vegetation and soil cracks; they forage principally on and near the soil surface; they are tolerant of and resistant to low air humidity; they make a nest with small heavily mudded cells which is likely to offer a substantial protection from drought and from the trampling of such small animals as rabbits; they remain in the nest most of the winter and thus retain control. The workers of *r* on the other hand have a build which fits them for quick movements over grass-herb vegetation; this enables them to work in the warmest stratum in sunny weather; they are less tolerant of and resistant to low humidities; they build a light nest which contains large irregular cells with little mud in the walls; and during winter they leave the summer nest altogether (this applies to *macrogyna*). No comparative measurements of colony reproductive potential have been made as this is an extremely difficult matter, yet it is conspicuously clear that more *r* come to the mating ground, and they come earlier in the summer. They are therefore certainly successful in the area and must exert a substantial population pressure towards vacant sites. But these adaptive differences are reinforced by interference which is as far as can be observed one-way—by *s* with *r*. They lay siege to *r* nests, render their workers impotent by removing their appendages, and devour their males. This must reinforce the

process of exploitative segregation, the more so because adaptation encourages colony growth, which as is well known increases aggressiveness. Further this, especially when combined with drought, is enough to cause *r* to evacuate, which means that *s* can take over the drier parts of areas already occupied by *r*; that is limited behavioural segregation is possible.

In this paper, emphasis has been laid on the two species of *Myrmica*, which occur together in grassland and are without question in the locality the only turf-nesting species (except for a few *M. lobicornis* Nyl.). Where bare areas of soil or soft wood, or large permanent stones exist, *Formica fusca* and *Leptothorax acervorum* occur as well. Before summarizing the position relating to this larger community it is necessary to add that Mr D. Muir (unpublished) has shown that the two species of *Myrmica* forage over longer periods and under a greater variety of weather conditions both by day and by night than *Formica fusca*, which only seems to forage in numbers when the weather is warm and sunny, usually in the middle of the day. The soil surface may in summer become too hot for *r* which then remain in their nests. These differences are certainly not forced by competition, for isolated colonies behave the same, but learned behaviour may sharpen the distinctions to some extent although there is at present no evidence for this.

Thus the various species fit into the community, which may be a very old boreal type, as polyphagous predators and tool-using plant consumers, in virtue of a number of differences in character which, either alone or with competition, have led to various degrees of segregation. *Formica fusca* is a large agile individual with large colonies, dominant for nest-site but limited by its lack of building skill, foraging less often, but ranging farther than the others in all three dimensions and able to monopolize fixed food sources at a much greater distance from its nest than the others. The *Myrmicae* are small slow-moving individuals, with small colonies, subdominant for nest-site but with more skill in building, foraging intensively, but for much longer periods and in worse weather. *Leptothorax acervorum* consists of even smaller individuals in even smaller colonies, totally lacking in aggressiveness but able to make nests in hard wood that are inaccessible to the larger species (an interactive segregation, for Elton & Miller (1954) have pointed out that in the absence of competitors this species nests in soft wood), foraging as widely as *Formica fusca*, but always as solitary individuals never as recruited groups. Talbot (1953) has indicated how a polyphagous community of American species in Michigan, fit together in virtue of differences in foraging level and temperature tolerance; competitive segregation does not seem to be involved.

Owing to the dominant role that ants play amongst terrestrial invertebrates except in boreal climates, accounts of their interspecific and intercolonial affairs are not lacking; Forel in particular may be mentioned as a pioneer. Haskins (1945) has given a graphic account of the changes in ant distribution that have followed in the wake of man. The island of Madeira has been the scene of two such changes in the past century: early in the nineteenth century *Pheidole megacephala* Forel began a replacement which was certainly complete by the middle of the century (Heer 1852, 1856); and it has since been replaced by *Iridomyrmex humilis* Emery

which is still expanding its range. It is noteworthy that although interference has played a considerable role in their success (e.g. the development of poison jets) it has always been backed by better feeding methods (related to the new human dominated ecosystems rather than the older non-human ones), by better colony organization (group action of small workers being more effective than individual action of large ones) and more plastic reproductive methods (pleometrosis and colony fission). Goetsch (1951) who has studied *I. humilis* in southern Italy emphasizes the fearless aggressivity of individuals and their highly developed capacity for group action. In the Gulf States of U.S.A. it has met with only limited success, the terrain being now divided between it (in the urban areas mostly) and an earlier invader from S. America *Solenopsis saevissima richteri* Forel (in rural localities mainly—Wilson 1951). It is not clear how extensive the competition is. More recently, Way (1933) has given several accounts of interaction between ants in E. Africa: in the coconut plantations there, the native *Oecophylla longinoda* Latr. is sometimes removed, destroyed and replaced by an immigrant from India, *Anoplolepis longipes* Jerd. In this case there is no evidence at all that the latter has a superior economy or even social organization. Indeed the converse may be the case, for *Oecophylla longinoda* keeps its trees freer from other insects including some species of ant (in small colonies of small individuals) and practises a form of controlled predation on Homoptera populations hitherto unrecorded for any ant.

There are a few studies of interrelations between other types of invertebrates that show similarities with the *Myrmica* results. In sewage beds the larvae of *Metriocnemus* (Chironomidae) are able partially to displace those of *Psychoda* (Psychodidae) from the upper layers; the mechanism involves predation (Lloyd, Graham & Reynoldson 1940, Lloyd 1943*a*, *b*). The larvae of the flesh-fly *Chrysomyia albiceps* can reduce the population of *C. chloropygia* by becoming predatory as the natural food-supply (dead meat) becomes short, and the larvae of the latter species common (Ullyett 1949). Two very closely related species of the grain weavil, *Calandra oryzae* L. called 'small' and 'large' are almost wholly segregated into wheat and maize respectively under 'natural' storage conditions. Birch (1954) has shown that each can live in both foods and that both prefer wheat for oviposition and indeed produce larger individuals so that segregation is certainly not selective. In spite of their preferences, the large ones have a higher innate capacity for increase in maize, and can maintain higher limiting populations in it than in wheat and the small species shows the same relation to wheat. In competition the small one eliminates the large one in wheat and the large the small in maize, as would be expected from the adaptive difference. Birch points out that there must be some other factor involved, for at the lower natural densities observed, and considering the time taken to effect a competitive segregation in the laboratory, one would expect quite a lot of overlap due to unresolved conflicts. Such cases of non-segregation are, as pointed out, common between the two *Myrmicae* in seral vegetation and disturbed habitats.

Very few of the many known instances of ecological segregation in verebrates (Huxley 1942, Lack 1944, Allee *et al.* 1949, Matthews 1952) have been analysed

with a view to determining how much is due to competition and how much to selection of habitat; the difficulty of experiment is of course much greater than with invertebrates. The two squirrels in Britain (*Sciurus vulgaris* and *S. carolinensis*) although much studied (see review by Shorten 1954) still leave an unresolved problem; direct hostility appears to be rare but other more refined methods of interference may exist and it should be recalled that in rats (Barnett 1955) exhaustion is commoner than injury. At the moment some form of exploitative competition, *S. carolinensis* occupying the sites vacated by *S. vulgaris*, appears to be in favour. There is strong circumstantial evidence that the two hares in Britain (*Lepus timidus* and *L. europaeus*) are segregated by competition (Matthews 1952) which does not seem to involve mutual hostility.

The food segregation of the cormorant and shag (Lack 1945) is likely to be due to selection of different feeding habitats but it is not known whether competition is involved. The feeding segregation of the British titmice of the genus *Parus* (Hartley 1953, Gibb 1954) is thought to be largely selective with associated structural differences. But at the time of year when it is most marked, in late winter when food is shortest, interspecies interference is greatest. Moreover, Snow (1949) has shown that the great tit (*P. major*) causes the crested (*P. cristatus*) and the willow (*P. atricapillus*) tits to forage lower in the tree canopy, and Hartley (1953) has evidence that the marsh tit (*P. palustris*) prevents the blue tit (*P. caeruleus*) foraging in the lower levels. Also Dixon (1954) has noted that the two species *Parus inornatus* and *P. rufescens* show no differential habitat selection, but the former which is the larger, forces the latter to breed in vacant or inferior sites. Pitelka (1951) has pointed out with Hummingbirds that 'a mutual but balanced depression of population levels of at least males occurred. In this interaction *Calypte anna* was favoured . . .' which indicates the complexities that may be encountered.

SUMMARY

1. The differences in local distribution of *Myrmica rubra* L. and *M. scabrinodis* Nyl. have been considered in western Scotland and compared with other regions.

2. Three examples of the partition of habitats between the two species have been described and evidence that they result from interactive segregation has been advanced.

3. Certain adaptive differences that prevent one species replacing the other entirely have been discussed and this situation compared with that in other animals.

REFERENCES

Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). *Principles of animal ecology*. Philadelphia.

Barnett, S. A. (1955). Competition among wild rats. *Nature, Lond.* **75**, 126-7.

Birch, L. C. (1954). Experiments on the relative abundance of two sibling species of grain weevils. *Aust. J. Zool.* **2**, 66-74.

Brian, M. V. & Brian, A. D. (1951). Insolation and ant population in the West of Scotland. *Trans. R. Ent. Soc. Lond.* **102**, 303-30.

Brian, M. V. & Brian, A. D. (1955). On the two forms *macrogyna* and *microgyna* of the ant *Myrmica rubra* L. *Evolution*, **9**, 280-90.
Brian, M. V. (**1952a**). Interaction between ant colonies at an artificial nest-site. *Ent. Mon. Mag.* **88**, 84-8.
Brian, M. V. (**1952b**). The structure of a dense natural ant population. *J. Anim. Ecol.* **21**, 12-24.
Brian, M. V. (**1955**). Food collection by a Scottish ant community. *J. Anim. Ecol.* **24**, 336-51.
Crombie, A. C. (**1945**). On competition between different species of graminivorous insects. *Proc. Roy. Soc.* (B) **132**, 362-95.
Crombie, A. C. (**1947**). Interspecific competition. *J. Anim. Ecol.* **16**, 44-73.
Darwin, C. R. (**1859**). *The origin of species by means of natural selection*. London.
Diver, C. (**1940**). The problem of closely related species living in the same area, in *The New Systematics*, ed. J. S. Huxley, Oxford.
Dixon, K. L. (**1954**). Some ecological relations of chickadees and titmice in central California. *Condor*, **56**, 113-24.
Elton, C. S. (**1932**). Orientation of the nests of *Formica truncorum* F. in North Norway. *J. Anim. Ecol.* **1**, 192-3.
Elton, C. S. & Miller, R. S. (**1954**). An ecological survey of animal communities : with a practical system of classifying habitats by structural characters. *J. Ecol.* **42**, 460-96.
Gibb, J. (**1954**). Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis*, **96**, 513-43.
Goetsch, W. (**1951**). Ameisen- und Termiten-Studien in Ischia, Capri und Neapel. *Zool. Jb. (Syst.)* **80**, 64-98.
Gösswald, K. (**1932**). Ökologische Studien über die Ameisenfauna des Mittleren Maingebietes. *Z. wiss. Zool.* **142**, 1-156.
Gösswald, K. (**1938**). Über den Einfluss von verschiedener Temperatur und Luftfeuchtigkeit auf die Lebensausserungen der Ameisen. 1. Die Lebensdauer ökologisch verschiedener Ameisenarten unter dem Einfluss bestimmter Luftfeuchtigkeit und Temperatur. *Z. wiss. Zool.* (A) **151**, 337-81.
Gösswald, K. (**1941**). Über den Einfluss von verschiendener Temperatur und Luftfeuchtigkeit auf die Lebensausserungen der Ameisen. 2. Über den Feuchtigkeitssinn ökologisch verschiedener Ameisenarten und seine Beziehungen zu Biotop, Woh- und Lebensweise. *Z. wiss. Zool.* (A) **154**, 247-344.
Hartley, P. H. T. (**1953**). An ecological study of the feeding habits of the English titmice. *J. Anim. Ecol.* **22**, 261-88.
Haskins, C. P. (**1945**). *Of ants and men*. London.
Heer, O. (**1852**). Über die Haus-Ameise Madeiras. *Naturf. Ges.* **54**, 1-24.
Heer, O. (**1856**). On the house-ant of Madeira (translated by R. T. Lowe). *Ann. Mag. Nat. Hist.* **17**, 209-24 and 322-33.
Huxley, J. (**1942**). *Evolution, the modern synthesis*. London.
Jacobson, H. (**1939**). Die Ameisenfauna des ostbaltischen Gebietes. *Z. Morph. Ökol. Tiere*, **35**, 389-454.
Lack, D. (**1944**). Ecological aspects of species formation in passerine birds. *Ibis*, **86**, 260-86.
Lack, D. (**1945**). The ecology of closely related species with special reference to the Cormorant (*Phalacrocorax carbo*) and Shag (*P. aristotelis*). *J. Anim. Ecol.* **14**, 12-16.
Lloyd, L., Graham, J. F. & Reynoldson, T. B. (**1940**). Materials for a study in animal competition. The fauna of the sewage bacteria beds. *Ann. Appl. Biol.* **27**, 122-50.
Lloyd, L. (**1943a**). Materials for a study in animal competition. The fauna of the sewage bacteria beds. *Ann. Appl. Biol.* **30**, 47-60.
Lloyd, L. (**1943b**). Materials for a study in animal competition. 3. The seasonal rhythm of *Psychoda alternata* Say, and an effect of intraspecific competition. *Ann. Appl. Biol.* **30**, 358-64.
Matthews, L. H. (**1952**). *British Mammals*. London.
Park, T. (**1954**). Experimental studies of interspecies competition. 2. Temperature, humidity and competition in two species of Tribolium. *Physiol. Zool.* **27**, 177-238.
Pitelka, F. A. (**1951**). Ecologic overlap and interspecific strife in breeding populations of Anna and Allen Hummingbirds. *Ecology*, **32**, 641-61.
Richards, O. W. & Waloff, N. (**1954**). Studies on the biology and population dynamics of British Grasshoppers. *Anti-locust Bulletin* 17.
Richards, S. J., Hagan, R. M. & McCalla, T. M. (**1952**). Soil temperature and plant growth, in *Soil physical conditions and plant growth*, ed. B. T. Shaw. New York.
Shorten, M. (**1954**). *Squirrels*. London.

Skwarra, E. (**1929**). Die Ameisenfauna des Zehlaubruches. *Schr. phys.-ökon. Ges. Königsb.* **66,** part 2.

Snow, D. W. (**1949**). Jämförande studier över våra mesarters näringssokande. *Var. Fägelv.* **8,** 156-69.

Talbot, M. (**1934**). Distribution of ant species in the Chicago region, with reference to ecological factors and physiological toleration. *Ecology,* **15,** 416-39.

Talbot, M. (**1953**). Ants of an old field community on the Edwin S. George reserve, Livingstone county, Michigan. *Contr. Lab. Vertebr. Biol. Univ. Mich.* No. 63, 13 pp.

Ullyett, G. C. (**1949**). Competition for food and allied phenomena in sheep blowfly populations. *Philos. Trans.* (B) **234,** 77-174.

Way, M. J. (**1953**). The relationship between certain ant species with particular reference to biological control of the Coreid, *Theraptus* sp. *Bull. Ent. Res.* **44,** 669-91.

Weber, N. A. (**1948**). A revision of the North American ants of the genus *Myrmica* Latr. with a synopsis of the paleartic species. 2. *Ann. Ent. Soc. Amer.* **41,** 267-308.

Westhoff, V. & Westhoff-de Joncheere, J. N. 1942 . Mededeeling van het comité ter bestudeering en bestrijding van insectenplagen in Bosschen : Number 9 : Verspreiding en nestoecologie van de mieren in de Nederlandsche Bosschen. *Tijdschr. Plzieht.* Sept.-Oct. 1942.

Wilson, E. O. (**1951**). Variation and adaptation in the imported fire-ant. *Evolution,* **5,** 68-79.

Yarrow, I. H. H. (**1954**). The British Ants allied to *Formica fusca* L. Hym., Formicidae. *Trans. Soc. Brit. Ent.* **11,** 229-44.

EXPLOITATION AND INTERFERENCE IN INTERSPECIES COMPETITION

By M. V. BRIAN
The Nature Conservancy, Furzebrook Research Station

(With 2 Figures in Text)

An ill-defined distinction between two forms of interspecies competition: exploitation (as Park 1954 has termed it) and interference has been maintained for more than a century (as Crombie 1947 has pointed out). Exploitation will be regarded here as the ability of a species to find, occupy and retain vacant vital resources. Interference will be regarded in its pure form as the ability of a species to damage another (assuming for simplicity that there are only two) either directly by attacking its individuals or indirectly by harming its resources or blocking its access to them; it does not necessarily use the same resources itself. Compounds of these two occur frequently, perhaps invariably in practice; for example, one species may oust another from its resources and then occupy them itself. Some authors maintain that only processes involving interference are 'truly competitive' (Crombie 1947, Elton & Miller 1954). However, competition is more usually applied to any interactive process even if indirect that leads to differential growth and survival (or natural selection as it is often termed). Further, the exploitation process is well known in human economics; it covers the efficiency of production and distribution and reaches a boundary with interference in advertising, a boundary that is fairly well defined by law, defamatory advertising being illegal in many countries.

In this paper certain mathematical models are re-examined in the light of this duality of the competition concept and interpretations are suggested that differ in some respects from those in the minds of the originators. It will appear that a distinction between the two forms of competition has been made, but never explicitly.

THE WINSOR MODEL

The model proposed by Winsor (1934) is one involving exploitation but not interference. Two species with population densities N_1 and N_2 compete for a third whose density is Z which serves as their food, and which is both limited and growth-limiting. Each species has constant increase (b_1 and b_2) and decrease coefficients (m_1 and m_2) and it will appear that the exploitation coefficients are compounds of these: for the first species, $b_1 m_2$; and for the second, $b_2 m_1$. The simultaneous differential equations are:

$$\mathrm{d}N_1/\mathrm{d}t = b_1 N_1 Z - m_1 N_1$$

$$\mathrm{d}N_2/\mathrm{d}t = b_2 N_2 Z - m_2 N_2$$

and the general solution in terms of the ratio of populations is:

$$N_1^{b_2}/N_2^{b_1} = \mathrm{C}\mathrm{e}^{(b_1 m_2 - b_2 m_1)t}$$

(C, a constant; t, time), indicating that, depending on the relative values of $b_1 m_2$ and $b_2 m_1$ the species density ratio increases to infinity or decreases to zero with time; that is the one having the superior exploitation power, drives the other out. This model has wide applicability and may be used when Z is not a food source, but any source that is essential (to which no alternatives exist) and it may even be a function of N_1 and N_2. The individuals of the population may be mobile searchers after a rain of food particles or they may seek fixed sites for nests in their youth, and then remain sedentary the rest of their lives. Since the latter is appropriate to many situations it may be considered a little further. An insulated area may have T sites all of which are occupied by one or other of the two species with the numbers N_1 and N_2 whose total is therefore T. The increase coefficients b_1 and b_2 must be regarded as including reproduction, discovery and establishment; the decrease coefficients may be similarly complex in conception but it is sufficient to regard them simply as intrinsic physiological survival coefficients. No interference (as defined) need enter into the situation at all.

In a small interval of time the number of sites becoming vacant (and hence available for recolonization) is v, and

$$v = m_1 N_1 + m_2 N_2;$$

if the population pressure is high, as it will be with saturating populations, these will be refilled immediately and the chance of the first species occupying any one is p, and it has the value:

$$p = b_1 N_1 \Big/ (b_1 N_1 + b_2 N_2).$$

Similarly the chance of N_2 is complementary (q) so that $p+q = 1$. And so, in each small interval of time the first species loses $m_1 N_1$ and gains pv and the second species loses $m_2 N_2$ and gains pv. These assumptions lead to a pair of equations like the others with the difference that

$$Z = (m_1 N_1 + m_2 N_2) / (b_1 N_1 + b_2 N_2)$$

The general solution is the same and the constant C has the value:

$$C = w^{b_2} T^{b_2 - b_1} / (1-w)^{b_1}$$

where wT is the population of N_1 at the start of observations.

Thus owing to the general solution being independent of Z this may either be independent (first example) or dependent on N_1 and N_2 (second example). In the latter case, the results depend on the site-tenacity of the species (expressed by m) and on the power of discovery (b). Skellam (1951) has considered a model similar in some respects but differing in that both species have no site-tenacity (rather, a series of discrete generations like annual organisms) and no site-localization capacity (their progeny are distributed at random). Even though one species is able to interfere successfully in the establishment of the other, this sub-dominant one is able to persist (if its reproductive potential is high enough) in the sites that the first has not, by chance, colonized.

The special case of the Winsor model that has been considered here is the deterministic analogue of one of the stochastic random walks (see Feller 1950). The

population of N_1 may in unit time, either rise by one unit, remain the same or increase by one unit. The chance of rising, p is given by:

$$p = \frac{m_2 N_2}{T} \cdot \frac{b_1 N_1}{T} \text{ and of falling, } q \text{ by: } \quad q = \frac{m_1 N_1}{T} \cdot \frac{b_2 N_2}{T}$$

so that the chance of staying at the same value, r is: $r = 1-p-q$. These transition probabilities ensure that the population remains within the limits 0 to T, and 'absorbing barriers' do not need to be postulated.

Since both p and q contain the factor $N_1 N_2 T^2$ their relative value is $m_2 N_2$, $m_1 N_1$. The common factor can accordingly be disposed of for the present purpose, whilst merely noting that it affects the rate of change not the direction of change. It is at a maximum when the two populations are equal, and declines towards zero as one or the other diminishes, so that the rate of change is greater when both species are nearly equal than when they are unequal. The difference equation and boundary conditions for the probability of N_1 winning (when it starts with a population of wT) symbolized p_{wt} are:

$$\begin{cases} p_{wT}(1-r) = pp_{wT+1} + qp_{wT-1}, & 1<wT<T-1 \\ p_0 = 0 \qquad p_T = 1 \end{cases}$$

whose explicit solutions are:

$$p_{wT} = (S^{wT}-1)/(S_T-1), \quad S = p/q, \quad p \neq q;$$
$$p_{wT} = w, \quad p = q.$$

Thus the chance of N_1 winning increases with its initial population, and in fact in the simple case when $p = q$ or $b_1 m_2 = b_2 m_1$ the chance is exactly w, carrying the implication that even when the two species, according to the deterministic model should co-exist in perpetual though unstable equilibrium, chance fluctuations will upset this. Further it may be noted that r like $N_1 N_2 T^2$ is irrelevant to the ultimate conclusion, affecting only the rate of interaction.

For the purpose of considering the question of species segregation it is useful to conceive the Winsor model not as a homogeneous area, but as a mosaic of two types of habitat. Each type is relevant to the animals that are competing and affects their exploitation coefficients in such a way that one is greater than the other in one type, and the converse situation exists in the other type. Alternatively, the set of sites may be strung out in a line across an environmental gradient that transposes the condition $b_1 m_2 > b_2 m_1$ into $b_1 m_2 < b_2 m_1$. As Crombie (1947) has pointed out, a sharp division is expected in theory but it will be blurred by chance and other factors in practice. Thus theory predicts that the dynamics of the populations themselves create pressures that ensure ultimate species purity in relation to sets of vital resources under equivalent environmental conditions.

THE LOTKA-VOLTERRA MODEL

The model given by the more usual competition equations due independently to Lotka and Volterra is radically different from the above one although originally

conceived, like it, as competition for common food resources. It includes no differential exploitation at all, merely interference between the species, a fact which is in effect the basis of the objection which Andrewartha & Birch (1953) have lodged against it. They feel that as long as there is no common resource, power over which is being sought by more than one species 'real competition' is not occurring. In fact the situation becomes more akin to partial mutual predation between polyphagers — which is, it must be recalled, far from uncommon in nature (amongst the predominantly predatory Formicidae for example).

In considering this model then, one must imagine the two species as having no resource in common at all; perhaps they are living in different sections of a mosaically heterogeneous habitat and indulging in mutual interference either by entering each other's area or by displaying on the boundary. Then if N_i is the density (this gives an implicit limitation to the resources which number would not do), b_i the coefficient of increase, K_i the limiting density, and c_i a parameter which represents the action equivalence of the two species, or their coefficients of interference, the equations may be expressed:

$$\frac{dN_1}{dt} = b_1 N_1\left[1 - \frac{1}{K_1}(N_1 + c_1 N_2)\right]$$

$$\frac{dN_2}{dt} = b_2 N_2\left[1 - \frac{1}{K_2}(N_2 + c_2 N_1)\right]$$

That is each grows in proportion to its population reduced by a fraction which involves the proportion of the maximum population that has been reached, measured in the appropriate units after conversion to equivalence through c_i. At the equilibrium (that is when $dN_i/d_t = 0$) the two species populations are:

$$N_1 = (K_1 - c_1 K_2)/(1 - c_1 c_2)$$
$$N_2 = (K_2 - c_2 K_1)/(1 - c_1 c_2)$$

which indicates steady states when neither exist (unstable) and when one or other exists alone (stable — Lotka 1932) and a state of co-existence (stable — Winsor 1934). The last alone is of interest in the present connection; it exists whenever $K_1 > c_1 K_2$ and $K_2 > c_2 K_1$ and hence $c_1 c_2 < 1$.

It is useful to vary the mutual interference of the species, by allowing c_1 and c_2 to change slowly in time or space subject to the condition $c_1 c_2 < 1$ and considering the separate and combined equilibrium populations. There are two cases: when the two coefficients are independent, and when they are correlated; but only the latter condition will be considered here. When correlation is positive, the model indicates that habitat structure or food distribution affects mutual interference (perhaps by increasing species interspersion) when correlation is negative the situation may be visualized as one in which the species are adapted to different ends of a scale in a physical factor so that at one end one is 'stronger' or more interfering and at the other the other is.

(a) Similar powers of interference

In the first case writing $c_2 = rc_1$, one obtains the equations

$$N_1 = (K_1 - c_1 K_2)/(1 - rc_1^2),$$
$$N_2 = (K_2 - rc_1 K_1)/(1 - rc_1^2)$$

both of which may be represented graphically by concave upwards curves (with c_i along the abscissa and N_i along the ordinate), with a single minimum when

$$c_1 = \frac{K_1}{K_2} - \sqrt{\left(\frac{K_1}{K_2}\right)^2 - \frac{1}{r}}, \text{ for } N_1$$

and

$$c_2 = \frac{K_2}{rK_1} - \sqrt{\left(\frac{rK_2}{rK_1}\right)^2 - \frac{1}{r}}, \text{ for } N_2.$$

Consider now increasing c_1 from zero: at zero, both N_1 and N_2 coexist at their maxima, K_1 and K_2 respectively. As it gets larger, that is as interference becomes more and more intense, the result depends on whether c_1 reaches a value K_1/K_2 before a value K_2/rK_1. If the former comes first, then $N_1 = 0$ and $N_2 = K_2$ if the latter then $N_1 = K_1$ and $N_2 = 0$, the converse situation. Clearly this implies that the relative values of K_1 and K_2 determine which species will survive as competitive interaction is increased, in other words when the c values are linked, success in competition goes to the species which utilizes the resources more efficiently. If it is agreed to select the case where

$$K_2/rK_1 < K_1/K_2$$

then it is seen that N_2 cannot have a minimum since the quantity under the square root is negative, that is $\frac{1}{r} < \left(\frac{K_2}{rK_1}\right)^2$ but N_1 has a minimum since the square root is real $\left(\frac{K_1}{K_2}\right)^2 > \frac{1}{r}$. Hence whilst N_1 starts at K_1, declines to a minimum at

$$\frac{K_1}{K_2} - \sqrt{\left(\frac{K_1}{K_2}\right)^2 - \frac{1}{r}}$$

and rises again to K_1 (Fig. 1), N_2 declines from K_2 to zero at first slowly, then after inflexion, more quickly. The decline in N_1 the stronger species, is interesting as it illustrates the material loss involved through interaction with a fairly strong competitor (the cost of interference). The total population can be shown to decline from $K_1 + K_2$ to K_1 at a decreasing rate along a non-inflecting curve that is concave upwards. It can also be shown that the dominant species increases its proportion in the population all the time even though it has a minimum actual value.

Thus as the structure of the environment is changed so as to increase mutual interference (and a conveniently visualizable change is an increasing degree of species interspersion), the two species that exist first at very near their own self-controlled population densities, both decline, then one declines whilst the other

rises back to its self-controlled value. The total population declines at first quickly and then more slowly and the proportion of the dominant species increases throughout.

(*b*) *Inverse powers of interference*

Coming now to the case in which the interference coefficients are negatively correlated so that the two species may be thought of as having different conditions of efficiency, it is convenient to assume that $c_1 c_2 = s$ a constant, so that the coefficients are related hyperbolically. Then at equilibrium the populations are:

$$N_1 = \frac{K_1}{1-s} - \frac{sK_2}{c_2(1-s)}$$

$$N_2 = \frac{K_2}{1-s} - \frac{sK_1}{c_1(1-s)}$$

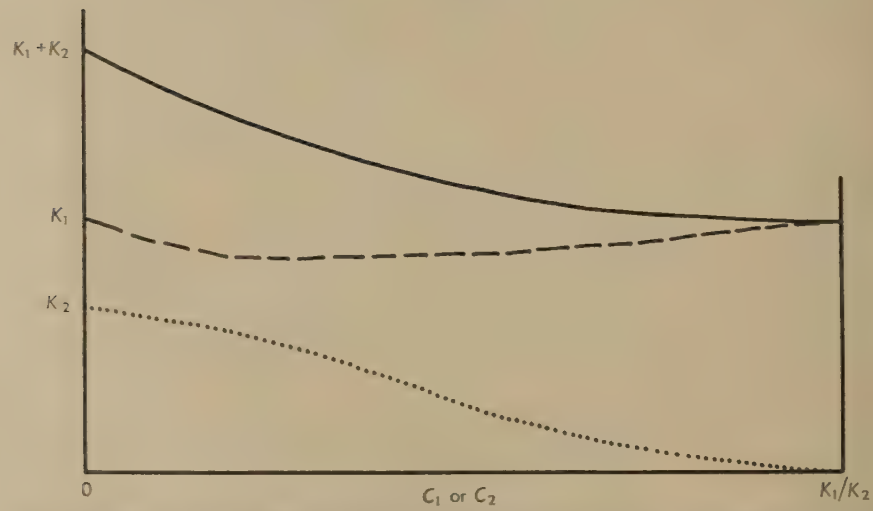


Fig. 1. Theoretical curves of the equilibrium populations (ordinate) of two competing species N_1 and N_2 when the competition coefficients (c_1 and c_2) are positively correlated and increase from 0 to $K_1 K_2$. For simplicity, $K_1 K_2 = 1{\cdot}5$ and $c_1 = c_2$. Full line = total population; broken line = N_1; and dotted line = N_2.

Each equation, N_1 with c_2 as independent variable, and N_2 with c_1 as independent variable then shows the populations rising at a slowing rate without inflexion (curve convex upwards) indicating that as their power of interference with the other increases their population benefits at first quickly, and then less and less as the limit K_1 or K_2 respectively is approached. The limit K_1 is reached when $c_2 = K_2 K_1$, and the limit K_2 is reached when $c_1 = K_1/K_2$. Viewed in reverse, the population density of the first species (N_1) which exists at a maximum as long as $c_2 \geqslant K_2 K_1$ declines to zero when c_2 is reduced to sK_2/K_1, the decline in each case being at an accelerated rate (curve convex upwards).

Since c_1 and c_2 are negatively correlated they can conveniently be represented on a chart (Fig. 2) with one increasing to the right and the other to the left, the product of any two scale readings connected by a vertical line being constant (with the value $c_1c_2 = s$). On this graph the population of the first species declines from its maximum to zero whilst concurrently that of the other rises to its maximum from zero. This overlap makes it quite clear that the total combined population

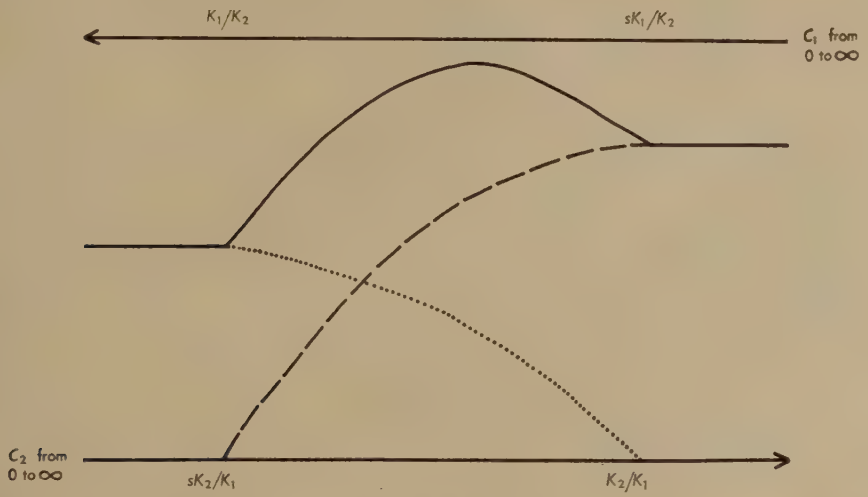


Fig. 2. Theoretical curves of the equilibrium populations (ordinate) of two competing species N^1 and N_2 when the competition coefficients (c_1 and c_2) are negatively correlated with product constant) and increase from zero to infinity. The lower abscissa increases from left to right, the upper one from right to left. Full line = total populations; broken line = N_1, and dotted line = N_2.

is greater than either alone (as pointed out by Andrewartha & Birch 1953). In fact it can be shown that the total follows a convex-upwards curve without inflexion having a maximum at $c_2/c_1 = K_2/K_1$. The conditions of overlap are affected by s for

$$\frac{\delta N_1}{\delta c_2} = \frac{sK_2}{c_2{}^2(1-s)} \text{ and } \frac{\delta N_2}{\delta c_1} = \frac{sK_1}{c_1{}^2(1-s)}$$

So that, as s tends to unity the rate of change of population tends to infinity, and a sharp transition zone from one pure culture to the other would be expected. On the other hand, when s tends to zero the change is very slow, and the maximum value of the combined populations approaches K_1+K_2. In the diagram these variations can be visualized by imagining the two scales sliding backwards and forwards over each other.

The first of these conditions, when s tends to unity, can of course be achieved by concomitant high values of c_1 and c_2; in the extreme case they may be unity. This converts the basic simultaneous differential equations into one of the family:

$$dN_1/dt = b_1N\left[1-\frac{1}{K_1}(hN_1+kN_2)\right]$$

$$dN_2/dt = b_2N_2\left[1-\frac{1}{K_2}(kN_2+hN_1)\right]$$

which is the group considered by Volterra (see D'Ancona 1954); in the present case, h and k are both unity. As Lotka (1932) pointed out, this does not permit coexistence in equilibrium. He commented: 'The physical significance of this is that both species consume one and the same food or if they consume a mixed diet, that proportion of each ingredient of the diet which they consume is the same for both species'. Only when the h and k coefficients are unequal in the two equations, so that $h_1 \neq h_2$ and $k_1 \neq k_2$ is stable co-existence possible. Relative to this state Lotka commented: 'This is more in keeping with the facts of nature since it is common knowledge that a great variety of species sharing sources of food do live together in essentially stable equilibrium'. According to the present thesis Volterra's system should more correctly be interpreted as meaning that between two species that did not compete for any common resource (no exploitative competition) the interference could be so intense and mutual that only one or other could exist in any area.

DISCUSSION

Thus the general Lotka-Volterra model is quite different from that of Winsor. The latter involves competition, by exploitation alone, for essential common resources. The former involves competition by interference alone, between species having no common resources. They represent the isolated components of the duel competition concept. Only the Winsor model predicts unconditional segregation in an environment that is heterogeneous in a way affecting the exploitation coefficients. The difference between these coefficients affects the rate of completion of the process. In the Lotka-Volterra model segregation is assumed to exist beforehand in a sense that does not preclude the possibility of interference, so that where segregation is on a small scale and the species are highly interspersed it can happen, especially if the interference coefficients are materially different, that a further larger scale segregation will devlop, although the resources vacated by the loser within these new areas will not be occupied by the winner but merely patrolled.

Time variations may be briefly considered here. As long as occupation of the resource units is continuous, then temporal periodicity in modifying factors that cause periods of quiescence, will only affect the rate of change in the spatial pattern (this will be proportional to the extent of overlap in the activity periods). Time trends, on the other hand, may change the situation radically and alter monopoly by one species into monopoly by the other. There can of course be no temporal segregation. When occupation is intermittant neither spatial nor temporal segregation can develop through demographic processes, although behavioural ones whether instinctive or learned may be effective.

ACKNOWLEDGMENT

The comments and criticism of Mr J. G. Skellam are gratefully acknowledged.

SUMMARY

The analysis of interspecies competition into two components, exploitation and interference, is examined from a theoretical point of view. It is suggested that two deterministic models exist which represent one or the other of these in pure form. A stochastic model of the exploitation type is described.

REFERENCES

Andrewartha, H. G. & Birch, L. C. (**1953**). The Lotka-Volterra theory of interspecific competition. *Aust. J. Zool.* **1**, 174-7.

Crombie, A. C. (**1947**). Interspecific competition. *J. Anim. Ecol.* **16**, 44-73.

D'Ancona, U. (**1954**). *The struggle for existence.* English translation by Anne Charles and R. F. J. Withers. Leiden.

Elton, C. S. & Miller, R. S. (**1954**). The ecological survey of animal communities : with a practical system of classifying habitats by structural characters. *J. Ecol.* **42**, 460-96.

Feller, W. (**1950**). *An introduction to probability theory and its applications.* New York.

Lotka, A. J. (**1932**). The growth of mixed populations, two species competing for a common food supply. *J. Wash. Acad. Sci.* **22**, 461-9.

Park, T. (**1954**). Experimental studies of interspecies competition. 2. Temperature, humidity and competition in two species of *Tribolium*. *Physiol. Zool.* **27**, 177-238.

Skellam, J. G. (**1951**). Random dispersal in theoretical population. *Biometrika*, **38**, 196-218.

Winsor, C. P. (**1934**). Mathematical analysis of the growth of mixed populations. *Cold Spr. Harb. Sym. Quant. Biol.* **2**, 181-7.

THE BIOLOGY OF *LEPTOCERUS** *ATERRIMUS* STEPH. WITH REFERENCE TO ITS AVAILABILITY AS A FOOD FOR TROUT

By N. C. MORGAN
Brown Trout Research Laboratory, Pitlochry

(With 5 Figures in the Text)

INTRODUCTION

Observations on the feeding of brown trout, *Salmo trutta* L., from lakes have shown that larvae of *Leptocerus aterrimus* form an important part of the diet in May, June and July. Allen (1938), in a study of the food of trout from Windermere throughout the year, showed that *Leptocerus* larvae became the characteristic food in May, June and July, forming 15·1% by numbers of the diet in May, 37·1% in June and 36·2% in July. Humphries (1936) refers to the *Leptocerus* in Windermere as *L. aterrimus*. Frost & Smyly (1952), working at Three Dubs Tarn, showed that *Leptocerus* larvae featured to the greatest extent in the food of trout in May and were also a common constituent in June, July and August. Macan (1949) records *L. aterrimus* as representing the genus in this tarn. Mr T. A. Stuart (personal communication) showed that in Loch Moraig, Perthshire, *L. aterrimus* larvae were taken in large numbers during June (Table 1). The present investigations at Loch Dunmore, Perthshire, during 1954, indicated that the trout were eating the greatest numbers of *L. aterrimus* larvae in May.

Table 1. *Occurrence of* Leptocerus aterrimus *larvae in trout stomachs; Loch Moraig, 1951*

	Number examined	Percentage containing larvae	Average number of larvae per stomach
24-30 April	4	50	2·5
1-15 May	16	88	7·8
16-31 May	9	89	11·0
1-15 June	10	60	10·0
16-30 June	18	100	58·7
1-15 July	7	42	9·7
16-31 July	9	55	1·1
1-15 Aug.	16	6	0·2
16-31 Aug.	10	10	0·4
1-15 Sept.	12	17	0·8
16-30 Sept.	9	44	1·0
1-15 Oct.	13	31	1·2

Allen (1938) considers the increase in importance of *L. aterrimus* from May to July to be due probably to their large size and increased activity before emerging. Frost & Smyly (1952) state that 'Trichopterous larvae, particularly *Leptocerus*, feature more prominently in all months than might be expected from the faunistic records'.

* Kimmings (1949) has renamed the genus *Leptocerus* Leach as *Athripsodes* Billberg.

The analysis of the stomach contents of trout caught on fly at Loch Moraig during July, August and September in 1954 is shown in Table 2. In July the greatest proportion of *L. aterrimus* eaten by trout are in the larval state but in August active pupae and imagines predominate. Two trout taken near the shore in August contained eleven and thirteen active pupae respectively. On several occasions trout were observed feeding on egg-laying adults of *L. aterrimus*, which were moving over the surface, while ignoring the sub-imagines of *Cloëon simile* Eaton which were sitting motionless on the surface and which are usually taken avidly.

Table 2. *Occurrence of various stages of* Leptocerus aterrimus *in trout stomachs; Loch Moraig, 1954*

	Number of stomachs examined	Average number/Stomach		
		Larvae	Active pupae	Imagines
July	10	16·2	0·4	0·6
August	12	0·5	2·5	2·2
September	10	1·5	0	0

Observations on the biology of *Leptocerus aterrimus* were started in order to discover whether the above observations on the feeding of trout, in particular the large number of larvae taken during May, June and July, were related to the behaviour of this caddis. The study was carried out in two Perthshire lochs, Loch Moraig and Loch Dunmore, during 1953 and 1954.

Loch Moraig is situated at a height of 1105 ft (337 m) among mountains which rise to about 3000 ft (915 m) and lies on a narrow wedge of limestone running between black schist. The loch is artificial in origin, having been formed by the damming of a stream which ran through a marsh. Two streams enter on the east side and there is a single effluent at the south-west corner. The surrounding countryside is moorland and the only shelter is provided by two wooded peninsulas and two wooded islands on the loch. The surface area of the loch is 37 acres (15 hectares), the average depth 5 ft (1·5 m) and the maximum depth 12 ft (3·7 m). The pH of the water has a summer range of 7·8-8·1 and a winter range of 7·5-7·9. The alkalinity ranges from 50-80 mg $CaCO_3$/l. in summer to 30-50 mg $CaCO_3$/l. in winter. The mud bottom of the loch is largely covered by *Chara hispida* L., but there are large beds of *Potamogeton natans* L. with scattered growths of *Myriophyllum spicatum* L. Around the shore *Chara aspera* Willden. and the emergents *Carex rostrata* Stokes and *Menyanthes trifoliata* L. are also found. The north, west and south shorelines are stony and the east shore is mainly silted.

Loch Dunmore lies at an altitude of 350 ft (107 m) and is situated in a wood. It is surrounded for the most part by *Rhododendron* bushes and well developed *Pinus sylvestris* L., *Picea abies* (L.) Karst., *Pseudotsuga taxifolia* (Poir.) Britt., *Larix decidua* Mill, *Betula pubescens* Ehrh. and *Fagus sylvatica* L. grow in the immediate vicinity. The surrounding ground consists of alluvium. The loch has been made by placing a dam across the neck of a small valley. In dry weather it is

fed by seepage but in wet weather a small stream also flows in. There is a single effluent at the north end. It is 4·5 acres (1·8 hectares) in extent with an average depth of 4 ft (1·2 m) and a maximum depth of 8 ft (2·4 m). In summer the pH varies from 7·3-7·7 and in winter from 6·9-7·4. Summer values for alkalinity are 25-28 mg $CaCO_3$/l. and in winter the alkalinity ranges between 20-30 mg $CaCO_3$/l. The bottom of the loch is composed of mud which, around the shoreline, is covered with dead leaves from the surrounding trees. The principal submerged macrophytes are *Potamogeton natans* L., *Nymphaea alba* L., *Myriophyllum spicatum* L., *Eleogiton fluitans* (L.) Link and *Apium inundatum* (L.) Rehb. The chief emergents are *Carex rostrata* Stokes, *Iris pseudacorus* L., and *Sparganium erectum* L.

METHODS

To estimate the number of larvae and pupae of *Leptocerus aterrimus*, trays were used in the shallow water of the stony shores down to a depth of 2 ft (0·6 m), and an Ekman grab in deeper water where the bottom was composed of mud. The trays, based on the type described by Moon (1935), consisted of a square wooden frame, internal area 1 sq. ft (929 sq. cm), across which was stretched a sheet of 'Tygan' screen cloth, 24 meshes to the inch. To simulate the surroundings they were filled with representative samples of the substratum dug from the region where they were to be used. The trays were laid firmly on the bottom and were left down for at least a fortnight before raising. The contents were then emptied into white photographic dishes and sorted in the field to remove the *L. aterrimus* larvae. The same stones, gravel and sand were used when the tray was replaced. The Ekman grab sampled an area of 42·25 sq. in. (273 sq. cm). The samples were sieved through a 40-mesh sieve, in the field, and taken to the laboratory for sorting.

Imagines were collected by means of sweep nets and in floating emergence cages (Adamstone & Harkness 1923, Scott & Opdyke 1941, Macan 1949). Three cages were used, two of which each covered an area of 5 sq. ft (0·46 sq. m) and one of which covered an area of 7·5 sq. ft (0·70 sq. m). The tops of these were covered with clear celluloid and the sides with 'Tygan' screen cloth, 24 meshes to the inch. Before emptying, the cages were lifted on to a board and taken to the shore, where the insects were removed in the boat-house. This minimized the entry and loss of insects.

Air temperature and water temperature, at a depth of 1 ft (0·3 m), were recorded in Loch Dunmore on a Negretti and Zambra 'Mersteel' temperature recorder.

THE EGG

Field observations showed that egg laying took place over the whole area of the lochs studied on calm days in June, July and August. The eggs were extruded from the tip of the abdomen of the female in a dark green mass about 1·5 mm in diameter. The egg mass was deposited on the water surface and sank to the bottom where it adhered to the plants or to the substratum. Swelling took place by the

uptake of water, so that the eggs became dispersed throughout a clear gelatinous sphere. This reached a diameter of about 4 mm 5 hours after laying and a diameter of 7 mm 24 hours after laying; thereafter the mass slowly increased in size, reaching a diameter of 8 or 9 mm by the time the eggs hatched. The spherical eggs containing green yolk were dispersed within the jelly except for a clear layer about 1 mm in depth at the surface. The mean diameter of the individual eggs was 0.28 mm. The measurements for eggs and the egg mass agree with those given by Ulmer (1909). The average number of eggs in eight egg masses was 149. Egg masses were collected in dredgings along the shoreline and from the deepest parts of the lochs.

It was found possible to pair *L. aterrimus* adults in glass crystallizing dishes 5 in. in diameter and 2½ in. high, providing they were given a rough surface, such as a stone, on which to crawl. Attempts to bring about pairing in larger glass tanks 16 × 11 × 21 in. were not as successful as in the smaller containers. The egg mass was deposited in shallow water in the tanks. Females enclosed in 3 × 1 in. glass tubes would often deposit the egg masses on the side of the tubes from where they could be transferred to water.

The development of the embryo could be observed under the microscope. At 15° C, which is about the average loch temperature in Perthshire for June and July, eggs took 9-16 days to hatch. The fully developed embryo lay curled in the chorion, dorsal surface outermost, and in its attempts to break out rotated and twisted, flexing its body and legs against the elastic chorion. No attempt to bite its way out of the chorion was observed although the mandibles were well developed. The chorion eventually split half way round and the larva escaped through this opening. Newly hatched larvae were 1 mm long.

THE LARVA

The young larva struggled through the jelly to the outside environment by twisting and flexing, using its legs to drag its way along, but again it did not use its mandibles to bite its way out. The larvae spent about a day in the jelly resting frequently between their efforts to get out. Undulation of the abdomen began towards the end of this period; this movement continued throughout larval and pupal life. On hatching the mandibles were the only heavily sclerotized region. The remains of the green yolk could be seen through the walls of the abdomen at this stage. When they had emerged from the egg mass the larvae immediately started to build a case from small sand grains. Unlike the case of older larvae this was usually wider at the posterior than at the anterior end (Fig. 2*a*), but a few were roughly parallel sided.

(*a*) *Habitat*

In Windermere, Moon (1934) found the larvae of *Leptocerus aterrimus* on the sandy shore as well as on rocks and stones, and Macan (1949) found the larvae among weeds and on mud, but not in the bog where *Limnophilus*, *Triaenodes* and *Phryganea* were present. In Loch Moraig larvae were taken on mud, along the

stony shore and on *Potamogeton natans*, *Myriophyllum spicatum*, *Chara hispida*, *C. aspera* and *Carex rostrata*. In Loch Dunmore they were collected from mud, among dead leaves and from *Apium inundatum*, *Eleogiton fluitans*, *Myriophyllum spicatum*, *Littorella uniflora*, *Sparganium minimum* (Hartm.) and *Potamogeton natans*.

The distribution of larvae in space and time was studied at Loch Moraig. Paired Ekman samples, from the mud bottom, were taken along a transect at right angles to the stony west shore, at depths of 4, 6, 8 and 10 ft (1·2, 1·8, 2·4 and 3·1 m) each month. Eight trays were laid in 1 ft (0·3 m) of water along the stony shoreline and up to the fringe of a *Carex rostrata* bed. These were raised each time the Ekman samples were taken, but during June, July and August they were also raised more frequently. The trays contained sand and gravel, and flat angular stones up to 8 in. (20 cm) across.

Table 3. *Numbers of larvae and pupae of* Leptocerus aterrimus *at various depths in Loch Moraig, 1953-54*

	Numbers/sq. ft				
	1 ft	4 ft	6 ft	8 ft	10 ft
6 October 1953	1	4	2	1	0
15 January 1954	0	12	3	3	—
11 March 1954	0	—	—	—	—
26 March 1954	1	—	6	0	0
29 April 1954	1	8	3	1·5	0
17 May 1954	1·2	—	—	—	—
4 June 1954	10·5	—	3	0	0
9 June 1954	9·2	—	3	0	0
14 June 1954	32	—	1·5	0	0
21 June 1954	26·5	—	0	0	0
28 June 1954	29·5	—	0	0	0
8 July 1954	47	—	1·5	0	0
16 July 1954	56	—	—	—	—
2 August 1954	29	—	—	—	—
10 August 1954	1·5	—	—	—	—
19 August 1954	3·7	—	—	—	—
3 September 1954	0·5	—	—	—	—

(— indicates no sample taken)

Egg masses and newly-hatched larvae were distributed down to a depth of 12 ft (3·7 m). From October to April larvae were found in the greatest numbers at 4-6 ft (1·2-1·8 m), though they occurred down to a depth of 8 ft (2·4 m) (Table 3). No larvae were found at a greater depth so that those hatching from eggs in deeper water must either migrate inshore or perish. Other investigators have found *L. aterrimus* larvae at greater depths, e.g. in Windermere, Humphries (1936) found these larvae to be common at 3 m, frequent at 6 m, rare at 12 m and absent below 12 m. In Esrom Lake, Berg (1938) found larvae of *Leptocerus cinereus* from 0-11 m, though they were most numerous on the stones near the shore where they averaged 50 per sq. m. He thought that in autumn the larvae possibly descended a little. During ice cover it has been noticed that *L. aterrimus* larvae are very difficult to find along the shoreline and they possibly descend into deeper water under these conditions.

In 1953 large numbers of larvae were taken in hand-net collections along the shore during June although very few had occurred in similar collections during

May. At the beginning of June 1954 there was an increase in the numbers of larvae in the trays in 1 ft (0·3 m) of water, and a reduction in the numbers in deeper water. This was associated with a migration of larvae inshore before pupation and large numbers of larvae pupated on the stones in the trays. Table 4 shows that larvae continued to migrate inshore until the end of July. After the formation of the pupal case the larva remains within it for six or seven days before moulting to form the pupa. Since 7% of the pupal cases contained larvae in this state on 2 August, it follows that there were still active larvae up to the end of July. Dredgings in 6 ft of water over mud in Loch Dunmore at the end of May showed that very few larvae were present although they had been plentiful at this depth earlier in the year. Pupae appeared on submerged twigs at the edge of this loch at the end of May. Moon (1936) found the larvae in great numbers on vertical rock walls a few weeks before pupation.

Table 4. *Stages in the life history of* Leptocerus aterrimus *taken on trays in Loch Moraig; May-August 1954*

Numbers present expressed as a percentage of the total catch on any one date

	Larvae	Pupal cases containg larvae	Pupal cases containing pupae	Empty pupal cases
17 May	**100**	—	—	—
4 June	**81**	19	—	—
9 June	**38**	46	16	—
14 June	**42**	**50**	8	—
21 June	**28**	**49**	23	—
28 June	**22**	24	**54**	—
16 July	**11**	33	**48**	8
2 August	—	7	**75**	18
10 August	—	—	30	70
19 August	1	—	9	**90**

An indication of the number of larvae migrating inshore is given by the occurrence of an average of 93 pupae/sq. ft on the trays in shallow water over the period 4 June to 2 August. Before this the number of larvae present on the trays was 1/sq. ft. The water temperature was 12·5° C on 17 May and 20·5° C on 4 June. The occurrence of an inshore migration was confirmed by an obvious increase in the numbers of *L. aterrimus* taken in hand-net collections, both along the stony shoreline and in *Carex rostrata* beds. The stones on the trays were originally collected from the surrounding substratum and there is no reason to suppose that these should be more attractive for pupation than those of the loch bottom surrounding the trays. The total number of pupae recorded from trays which were raised frequently during the pupation period was of the same order as the total from trays which were left down over the whole period.

(*b*) *Growth*

The growth of larvae taken from Loch Moraig is shown in Fig. 1 from which it will be seen that the records made are based on determinations of wet weight.

This criterion of growth seems preferable to length measurements as the latter can be influenced markedly by the degree of contraction of the larvae. Further, growth increments are shown more clearly by the increases in weight than by increase in length. To determine wet weight, the larvae were removed from their cases, dried on filter paper until the surface was no longer wetted and then weighed in stoppered weighing bottles. Each batch of larvae was weighed to the nearest milligram and each point shown in Fig. 1 represents the average of at least ten larvae.

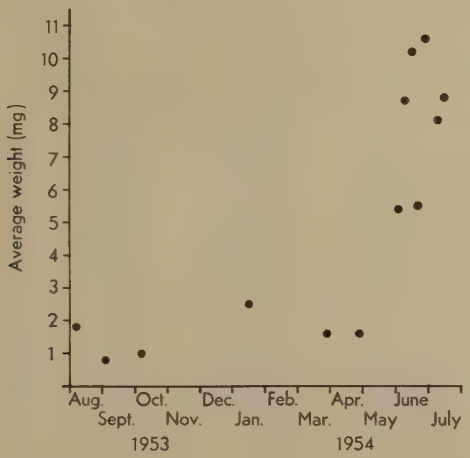


Fig. 1. Growth of *Leptocerus aterrimus* larvae as shown by measurement of wet weight.

The newly-hatched larvae grew until October but there was little growth from then onwards until the following May. A collection of larvae taken in October shows a considerable size-range, which is produced because egg-laying extends from July to August or later, and the larvae which hatch from eggs laid early have a longer period for growth before the onset of winter. This size-range persists throughout larval life; in October they ranged from 2·5 to 5·3 mm in length, in April from 1·9 to 4·5 mm and in June from 6·3 to 9·4 mm. Growth-rate increases considerably during May and remains high until pupation occurs in June and July. The absence of any appreciable growth from October to May may be due to the low water temperature (in the lochs studied the water temperature did not rise above 7° C between mid-October and mid-April) or to different feeding over the winter months. Investigations are being made on the feeding habits of this larva, which may clarify this point.

As previous investigators have used length measurements as a criterion of growth the results presented in Fig. 1 cannot be compared with those of other workers. The largest larva measured in the present study had a length of 9·7 mm; Ulmer (1909) gives the length of fully-grown larvae in Germany as 11·0 mm.

(*c*) *The larval case*

The changes in shape of the case throughout larval life are illustrated in Fig. 2. The newly-hatched larva forms a case 1·5 mm long which is normally wider at the posterior than at the anterior end (Fig. 2*a*). It is composed chiefly of sand grains but in a few instances pieces of algae are incorporated. In a week to ten days the case has taken on the form shown in Fig. 2*b*; the sides are now almost parallel and it is composed entirely of sand grains. The case is increased in size by the addition of sand grains to the anterior end (Figs. 2*c*, *d*) and it becomes a slightly curved, narrow, truncated cone as shown in Fig. 2*e*. Fig. 2*d* shows the typical shape during

Fig. 2. The changes in shape of the case of *Leptocerus aterrimus* during larval life and pupation: *a*, 25 July 1953, case of newly-hatched larva; *b*, 5 August 1953; *c*, 8 September 1953; *d*, 10 December 1953; *e*, 17 May 1954; *f*, 10 June 1954; *g*, 14 June 1954; *h*, 14 June 1954, pupal case; *i*, 5 July 1954, empty case.

the winter. The fully-developed larval case is similar to that in Fig. 2*f*. The tip of the case is generally broken off later and the case of a larva which is about to pupate is as shown in Fig. 2*g*. McLachlan (1874-80) (quoted by Miall 1903, p. 258) states that the tail end of the case is cut off before pupation. The chances of observing this are very slight and the operation was not observed in this study. The case is carried with the concave surface downward so that it is dragged along on the posterior tip. It will be noted from Fig. 2 that the posterior end of the case becomes wider as the case increases in length, and it is probable that this takes place by the wearing away of the posterior tip. The type of case shown in Fig. 2*f* is more fragile and the narrow tip could easily be broken off, to give the form shown in Fig. 2*g*, as the larva moves about. On the case shown in Fig. 2*g* there are a number of sand grains above the anterior aperture. These are not added until the larva is ready to pupate. Sometimes these are added while the case is of the form shown in Fig. 2*f*.

Hickin (1943) records the cases of larvae from a canal near Birmingham as 18 mm long, and Ulmer (1909) records them as 15-17 mm long in Germany. The longest case collected from Loch Moraig was 14·6 mm long.

(*d*) *Resting periods*

Larvae kept in the laboratory were frequently observed to attach the anterior end of their cases to plants or the glass side of the aquarium and to remain suspended with the metathoracic legs protruding and the head withdrawn into the case. One larva was observed to remain in this position for 33 days but the period was usually much shorter. The guts of some of these larvae were examined and were all found to be empty of food. It was first thought that the larvae were about to moult, but no cast skins or larvae in which the integument had not hardened after moulting were found.

THE PUPA

The majority of larvae in Loch Moraig pupated on the stones of the shoreline, but considerable numbers fastened their pupal cases to the stems of *Carex rostrata* in shallow water, and a few pupated under the floating leaves or on the upper part of the long stems of *Potamogeton natans* growing in 4-6 ft (1·2-1·8 m) of water. In order to test whether the prepupation movement of the larvae was initiated by an attraction towards light, experiments were carried out in which larvae about to pupate were kept in long troughs with one end towards a source of light and the other shaded. The larvae showed random movements and eventually pupated at both ends of the trough, wherever they found a rough surface, suggesting that they were not attracted to the light.

In Loch Dunmore where the bottom in shallow water is composed of mud and leaves the larvae pupated chiefly on twigs which had fallen into the water. Occasionally pupal cases were found on aquatic plants. It was noticeable that the pupae showed a marked tendency to aggregate, the pupal cases lying parallel and often several layers deep so as to form clusters. The rough surface, offered by the cases of the insects which had already pupated, would provide a suitable surface for attachment.

The pupating larva attaches the anterior end of the case to the substratum, by means of the silk gland secretion, and then reverses in its case and attaches the posterior end, so that, when the larva pupates on a vertical surface the anterior end of the case is usually uppermost. The larva then breaks off the sand grains carried above the anterior end of the case and proceeds to seal the aperture. It then reverses and closes the posterior end of the case with sand grains taken from the case itself (Fig. 2*h*). A small circular aperture is left in either end which is neatly rounded off with the hardened secretion of the silk gland as was recorded by Rousseau (1921, p. 601) for most of the Leptoceridae. This allows the anterior-posterior passage of the respiratory current. The rate of flow of this water current was measured by the use of dyes which showed that the water within the case was

replaced every fifteen seconds. In the laboratory larvae took about a day to attach and seal the pupal case.

The seal at the anterior end of the pupal case can be broken away easily by applying pressure with a mounted needle. It comes away neatly along the join of the newly-attached sand grains with the old anterior edge of the larval case. These sand grains do not interlock with those of the larval case and leave a line of weakness running round the case. This allows the emerging pupa to remove the end of the case easily. It is possible that the pupa may prize open the end of the case along this line, with its mandibles, rather than cutting it off. The end often remains hinged to the case at one point as shown in Fig. 2*i*. Ulmer (1909) records the pupal cases as 7-11 mm long and the pupae as 7·5-11 mm long. Pupal cases (Fig. 2*h*) from the lochs studied were 7·7-9·5 mm long and the pupae 7·4-9·5 mm long. The anterior aperture was 0·3-0·4 mm in diameter and the posterior aperture 0·4-0·5 mm in diameter.

After sealing the pupal case the insect remained in the larval state for 6 or 7 days and then pupated with the head towards the anterior end of the case and the anal appendages projecting through the posterior aperture. The ends of the long antennae were coiled around the tip of the abdomen. At 15° C the pupation period lasted from 8-18 days so that the shortest possible period spent in the pupal case, for the forty insects studied, was 14 days and the longest possible period 25 days. In 1953 pupae were found in Loch Moraig up to 11 August. During 1954 they were found from 9 June until 19 August (Table 4). In Loch Dunmore at a lower altitude pupation occurred about a month earlier.

Emergence was observed in the field and in the laboratory. After leaving the pupal case the active pupa swam rapidly to the water surface through which it thrust its prothorax so that it was held in the surface film by surface tension. The pupa then arched its thorax and undulated its abdomen vigorously. A few seconds later the cuticle of the pronotum split longitudinally and emergence followed.

It was observed in the laboratory that the active pupae were strongly attracted to light. If kept in a glass vessel, illuminated from the side, they would repeatedly drive themselves against the side towards the light, eventually dying owing to failure to reach the water surface. If the sides of the vessel were painted black, the active pupae swam straight to the lighted surface and emerged. In the field emerging pupae were observed to swim direct to the surface; thus they are presumably only available to predators for a very short period.

In the laboratory and on one occasion in the field imagines were found which had not been able to expand their wings during emergence, the wings remaining crumpled. This possibly occurs more frequently in the field than observed, since such individuals would rapidly fall prey to predators before they could swim to the shore. The newly-emerged adults spent several minutes on the water with the wings splayed out slightly and the antennae curved backwards, making feeble efforts to fly. Adults which have just emerged can be recognized by the pronounced curve of the antennae which become straighter a few hours after emergence.

THE IMAGO

(*a*) *Swarming*

Adult *L. aterrimus* are conspicuous during the emergence period owing to their habit of swarming. Swarming occurred in a band along the shore, stretching 3 or 4 ft (about 1 m) from the bank and not rising more than 3 or 4 ft above the water. Close observation showed that the individuals composing the swarms were not flying continuously but were making short excursions from the herbage, moving erratically among the other members of the swarm and then returning to the shore. Hand-net collections showed that the swarms were composed principally of males; out of 372 insects examined 336 were males. Berg (1938), referring to *Leptocerus cinereus*, states that they swarm from July to August near the shore. This species flew mostly 0·5-1 m above the water and the dense swarms generally form a belt less than 100 m broad along the shore.

Swarming occurred between 0745 h and 2030 h B.S.T. during July. At 0745 h the air temperature was rising rapidly and at 2030 h it was falling rapidly. Swarming only occurred when conditions were equable. The imagines were very sensitive to wind and on a day when the wind fluctuated they appeared suddenly when the wind dropped and disappeared as quickly to the shelter of the herbage when it rose. Although they often swarmed in sunshine a slight breeze would stop them. On windy days they were to be found swarming in the lea of wooded islands and peninsulas, and on several occasions they were observed swarming in light rain. The minimum air temperature at which adults were observed swarming was 14° C but possibly they will swarm at lower air temperatures. The only time imagines have been observed swarming outside the period shown above was during the night of 6-7 July 1955 when the air temperature remained unusually high, not falling below 17° C. Imagines were then seen swarming up to 2200 h and began swarming again at 0430 h.

(*b*) *Pairing and egg-laying*

On 2 August 1954 large numbers of *Leptocerus aterrimus* were observed emerging at 1200 h from Loch Moraig. The boat was moored in the lea of a wooded peninsula and soon about twenty *L. aterrimus* imagines had settled on the stern. These were mostly females but there were two pairs *in copula*. Soon other males, which were swarming nearby, landed on the boat and walked about the stern feeling from side to side with their long antennae, the tips of which were tapped lightly over the surface. When a male touched a female with its antennae, it immediately pursued the female over the surface of the boat. If the female was ready to pair it responded by vibrating its half-open wings, whereupon mating took place, the pair rapidly interlocking their genitalia and the male swinging round so as to face the opposite direction to the female. Most of the females *in copula* were newly emerged. Some females which had apparently paired responded to the advances of the male by flying away. Imagines were not seen flying *in copula*.

It is of interest to note that on two occasions male *L. aterrimus* were observed unsuccessfully attempting to pair with female *Oecetis lacustris* Pict., which also belong to the Leptocerinae. A female, taken from an emergence trap, deposited an egg mass in a 3 × 1 in. specimen tube within three hours of emerging. These eggs were infertile but appeared mature. It may therefore be that egg-laying can begin very soon after emergence.

Egg-laying was also observed in the field. The single egg mass, extruded from the tip of the abdomen, was deposited in the water by dipping the end of the abdomen into the water. The female rested on the surface for a few seconds and then fluttered on and off three or four times trying to wash off the egg mass. It then flew on a few yards and tried again until the eggs were deposited. Females were only seen egg-laying during calm weather.

(*c*) *Emergence period*

Information on the seasonal pattern of emergence was obtained from the floating emergence traps on Loch Dunmore. *Leptocerus aterrimus* imagines were only taken in the two traps over 1 ft (0.3 m) of water. None appeared in the third trap which was situated over 6 ft (1·8 m) of water, where there was a sparse growth of

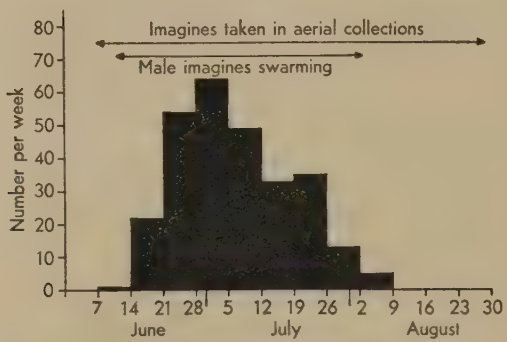


Fig. 3. Weekly totals of *Leptocerus aterrimus* taken in emergence traps.

Myriophyllum spicatum on a mud bottom. Fig. 3 shows the pattern of emergence during 1954, the total period lasting nine weeks. Emergence commenced in the second week in June, the numbers increasing rapidly during the third and fourth weeks. The highest rate of emergence occurred in the first week in July and then fell away steadily to the end of the first week in August. The water temperature over this period is given in Fig. 4. The period over which the adults were taken in hand-net collections is shown above the histogram, and it will be noted that the period over which male swarms were observed coincides with that over which the emergence rate was highest. The last adult taken in the hand-net collections was a male on 28 August before which none had been taken since 19 August. Newly emerged adults have been kept alive for seven days in the laboratory, without

food, and in the field the majority of adults had disappeared ten days after the last recorded emergence. Egg-laying is at its peak over the swarming period.

Ulmer (1909) records that *L. aterrimus* emerges during June, July and August in Germany; Moon (1936) records emergence at Windermere during June; Brundin (1949) records an emergence on 11 July 1943 in high Swedish lakes; and Macan (1949) during the weeks 9-16 July and 6-13 August at Three Dubs Tarn.

At Loch Moraig in 1953 adults were not present on 23 June and were first taken in collections on the next visit to the loch on 9 July. In 1954 they were not present in collections on 28 June and were first collected on 8 July. Small swarms were

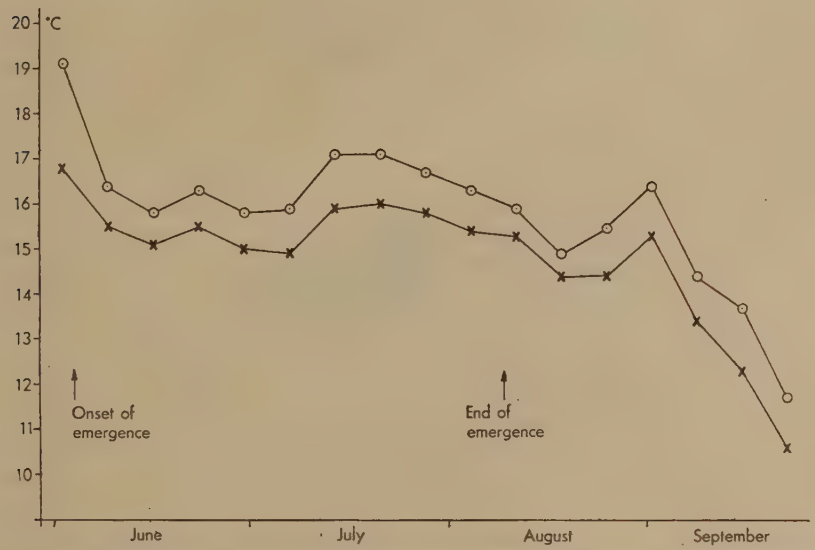


Fig. 4. Water temperature of Loch Dunmore in shallow water (1 ft depth); June-September 1954. (Weekly means of daily maxima and minima.)

still present on 3 September, but no imagines were collected on or after 15 September. Emergence in Loch Dunmore, at a lower altitude, was thus about a month ahead of Loch Moraig. It commenced at both lochs when the mean daily water temperature was about 16° C. In Loch Dunmore the mean water temperature was still about 16° C at the end of the emergence period (Fig. 4) but at Loch Moraig it had fallen to 12° C.

In Loch Dunmore 276 adults emerged from an area of 12·5 sq. ft (1·2 sq. m) giving an average of 22/sq. ft (239/sq. m). This is lower than from Loch Moraig but no valid comparison can be made as the density of pupation over a given area depends very much on the nature of the substratum.

Diurnal variation in emergence is shown in Fig. 5. The traps were visited every two hours on 9, 12, 13, 14, 22 and 23 July on which days a total of 49 insects were taken. It will be seen that the majority of the *L. aterrimus* emerged between 0800 h

and 1800 h B.S.T., a period when the water temperature is rising and when the light intensity is highest. All but one of the insects collected emerged during the hours of daylight, but although it was light between 0400 and 0800 h, no *L. aterrimus* were taken in emergence traps. No swarming was observed over this period when air and water temperatures were lowest. At night the adults were found sheltering on the leaves of the bushes surrounding the loch. There is an indication of maximum emergence occurring between 0800 and 1200 h. Though this is not statistically significant, possibly numbers of pupae become ready to emerge overnight and do so when conditions become favourable. More results

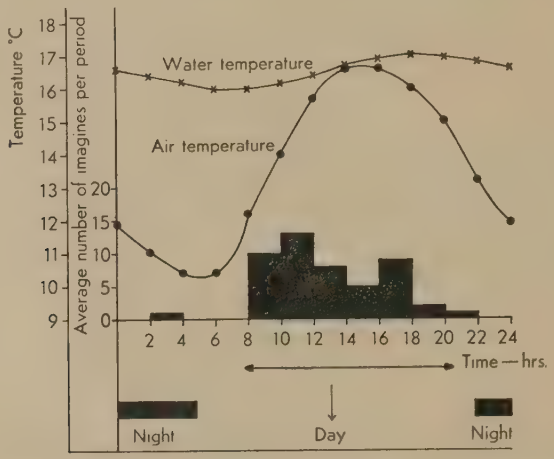


Fig. 5. Diurnal variation in emergence of *Leptocerus aterrimus* from Loch Dunmore, 1954. The vertical arrow indicates the time at which the sun was at its zenith, the horizontal arrows the time during which the imagines swarm.

would be required to confirm this and to indicate whether the secondary peak between 1600 and 1800 h is significant. The diurnal emergence period coincides closely with the time during which the imagines swarm, when air temperatures are at their highest. These conditions are favourable for the newly-emerged imago, and the males swarming near the banks can pair with the newly-emerged females which fly to the shore.

Table 5. *The numbers of male and female* Leptocerus aterrimus *taken in emergence traps on Loch Dunmore in 1954*

Period	Male	Female
14-30 June	63	30
1-19 July	67	42
20 July-9 August	36	25
Totals	166	97

The ratio of males to females taken in emergence traps was roughly 5 : 3 (Table 5). Statistical analysis of these results indicates that the proportion of males in the whole population for the total period of emergence lies between 0·57 and 0·69 for

95% confidence limits. The proportions of males in the three periods shown in Table 5 do not differ significantly. This preponderance of males may well be connected with the mating swarms which form a characteristic part of mating behaviour.

(*d*) *Colour variations*

Ulmer (1909) noted a form with light-coloured forewings and in the present study considerable variation in the colour of the forewings, from light reddish-brown to almost black, was noticed. This was not related to sex nor to the length of time since the imagines had emerged. Dark and light forms were noted in newly-emerged adults. There was no temporal difference, both forms occurring throughout the emergence period. The dark and light forms interbred freely. Mosely (1939) suggests that the light-coloured form may be the variety *tineoides of* Scopoli.

PREDATION BY TROUT

The large numbers of *Leptocerus aterrimus* larvae eaten by brown trout in May, June and July can be correlated with the movement inshore of the larvae which are about to pupate. The larvae are then fully grown, and this combined with their active movement inshore will make them more obvious to fish predators, which hunt their food by sight, than at other time of the year. Migration inshore may commence in May or June and the time of increase in numbers in the stomach of trout varies in accordance with this. Frost & Smyly (1952) state that *Leptocerus* features more prominently as a trout food throughout the year than might be expected from the faunistic records. Observations on larvae in aquaria show that they actively climb the submerged vegetation and attract attention as the rigid case waves about. This may serve to make them an easy prey to trout. *L. aterrimus* larvae probably have few insect predators, being well protected by their cases, and trout must be considered one of their chief enemies.

Mr T. A. Stuart (personal communication) noted that *L. aterrimus* larvae often occur in trout stomachs with *Cloëon simile* larvae and imagines, chironomid larvae and pupae, *Haliplus* larvae, spruce and larch needles and small splinters of wood. He observed that the trout commence feeding at the water surface and move down the rising stream of *C. simile* larvae and chironomid pupae until they are feeding off the bottom. Here they encounter *Haliplus* larvae and *L. aterrimus* larvae of about the same size and commence feeding on these. Stuart records that the trout are feeding on a certain size of food and hence conifer needles and small splinters of wood, about the same size and shape as the *L. aterrimus* cases are eaten at the same time.

Active pupae are only available to trout for a short time when they emerge in the shallower regions of lakes near the shore, and trout feeding in shallow water are able to catch the active pupae as they make the short excursion from the safety of their pupal case to the water surface. Newly-emerged imagines are also available over shallow water before they fly to the shore. Egg-laying imagines are

available to trout feeding at the surface over the whole area of small lakes from June to August.

Some other species of aquatic insects probably become more available as trout food when undergoing migrations. Thus the large numbers of the larvae of *Sialis lutaria* L. often taken by trout in March in Three Dubs Tarn (Frost & Smyly 1952), and in March and April in Loch Tummel (Mr R. N. Campbell, personal communication), are probably due to a migration inshore. Berg (1938) in his investigations on Esrom Lake found that for most of the year the larvae of *S. lutaria* were distributed from 0-12 m, being present in the greatest numbers at about 8 m. In March he found large larvae under almost every stone along the shore having moved inshore ready to pupate in April, May and early June.

SUMMARY

1. Observations on the feeding of *Salmo trutta* L. on *Leptocerus aterrimus* are reviewed and it is shown that it is taken most readily by trout during May, June and July while still in the larval state.

2. The biology of *Leptocerus aterrimus* has been studied in two Perthshire lochs, Loch Moraig and Loch Dunmore.

3. Eggs were laid in June, July and August and distributed throughout the lochs in spherical egg masses which each contained about 150 eggs. The young hatched out in 9-16 days at 15° C. They did not bite their way out of the egg or egg masses although their mandibles were well developed.

4. During most of the year larvae were distributed down to a depth of 8 ft (2·4 m) at Loch Moraig, but during June and July they migrated into 1-2 ft (0·3-0·6 m) of water before pupation. In Loch Moraig pupation occurred between the second week of June and the third week of August in 1954. An average of 93 larvae pupated per sq. ft (1001/sq. m) during this period, whereas there was an average of 1 larva/sq. ft (11/sq. m) at depths of 1-2 ft (0·3-0·6 m) in May.

5. The egg-laying period lasts ten weeks so that there is a considerable size-range in the larvae by October. This size-range can be traced throughout the winter and following spring. There is little growth from October to April but growth is rapid in May and June. Weight measurements, as compared with length measurements, give a better measure of growth in Trichoptera larvae. Changes in shape of the larval case are described.

6. Pupation site and the method of attachment and sealing of the pupal case are described. At 15° C the insect remained in the larval state, within the closed pupal case, for 6-7 days and then pupated. They spent 8-18 days as pupae. There is a line of weakness around the anterior end of the pupal case along which it is severed before emergence. Active pupae were strongly attracted to light and swam direct to the water surface to emerge.

7. In Loch Dunmore emergence occurred between 7 June and 9 August in 1954, reaching a peak during the first week in July. In Loch Moraig, at a higher altitude, emergence was a month later occurring between the beginning of July and the beginning of September.

Emergence took place primarily between 0800 and 1800 h B.S.T. The water temperature is rising during this period and the sun is at its zenith in the middle of it.

8. Male imagines swarmed along the bank between 0745 and 2030 h B.S.T. This is the warmest period of the day in July. Swarming *L. aterrimus* were very sensitive to wind. Mating can take place soon after emergence and pairing occurs on the ground. The eggs are deposited by 'dipping'.

9. The ratio of male to female imagines is approximately 5 : 3 over the whole emergence period.

10. The feeding of *Salmo trutta* on *Leptocerus aterrimus* is discussed. Trout take the larvae in large numbers from May to July when they are migrating inshore. They are then at their largest and are more active at the summer temperatures. Active pupae and imagines are taken from June to August when they are available in large numbers. Imagines are most vulnerable when newly emerged and when the females are egg-laying. It is suggested that other insects (e.g. *Sialis lutaria*) are also more available to trout when the larvae are migrating.

REFERENCES

Adamstone, F. B. & Harkness, W. J. K. (1923). The bottom organisms of Lake Nipigon *Publ. Ont. Fish. Res. Lab.* No. 15, 48 pp.

Allen, K. R. (1938). Some observations on the biology of the trout (*Salmo trutta*) in Windermere. *J. Anim. Ecol.* **7**, 333-49.

Berg, K. (1938). Studies on the bottom animals of Esrom Lake. *K. danske vidensk. Selsk. Skr.* **8**, 1-255.

Brundin, L. (1949). Chironomiden und andere Bodentiere der sudschwedischen Urgebirgsseen. *Rep. Inst. Freshw. Res. Drottning.* No. 30.

Frost, W. E. & Smyly, W. J. P. (1952). The brown trout of a moorland fish pond. *J. Anim. Ecol.* **21**, 62-86.

Hickin, N. E. (1943). Larvae of the British Trichoptera. 18. *Leptocerus aterrimus* Steph. (Leptoceridae). *Proc. R. Ent. Soc. Lond.* (A) **18**, 106-8.

Humphries, C. F. (1936). An investigation of the profundal and sublittoral fauna of Windermere. *J. Anim. Ecol.* **5**, 29-52.

Kimmins, D. E. (1949). Some changes in generic names in the family Leptoceridae (Order Trichoptera). *Entomologist*, **82**, 201-4.

Macan, T. T. (1949). Survey of a moorland fish pond. *J. Anim. Ecol.* **18**, 160-86.

Miall, L. C. (1903). *The Natural History of Aquatic Insects.* London.

Moon, H. P. (1934). An investigation of the littoral region of Windermere. *J. Anim. Ecol.* **3**, 8-28.

Moon, H. P. (1935). Methods and apparatus suitable for the investigation of the stony littoral of oligotrophic lakes. *Int. Rev. Hydrobiol.* **32**, 319-33.

Moon, H. P. (1936). The shallow littoral region of a bay at the north-west end of Windermere. *Proc. Zool. Soc. Lond.* 1936, 491-515.

Mosely, M. E. (1939). *The British Caddis Flies (Trichoptera).* London.

Rousseau, E. (1921). *Les Larves et Nymphes aquatiques des Insectes d'Europe.* Bruxelles.

Scott, W. & Opdyke, D. F. (1941). The emergence of insects from Winona Lake. *Invest. Ind. Lakes*, **2**, 4-14.

Ulmer, G. (1909). *Die Süsswasserfauna Deutschlands.* Pts. 5 and 6 : *Trichoptera.* Jena.

NOTES ON THE ANALYSIS OF SHALLOW-WATER SOFT SUBSTRATA

By J. F. C. MORGANS

Department of Zoology, University of Cape Town

(With 2 Figures in the Text)

It has long been recognized that the nature of the substratum is of the greatest importance in determining the nature of the bottom flora and fauna. There is a striking difference between the biota of rocks and of soft bottoms whether observed intertidally or sampled by dredging. Again, the various soft bottoms such as gravels, sands and muds show differences in biota and it is natural to try to relate these differences to local substratum characteristics. Various features of soft substrata have received attention as being of particular importance to the biota. As long ago as 1891 Murray & Renard analysed substrata with regard to mineralogical constitution and particle size and these features have since received more attention. However, interest in mineralogical analysis has dwindled because the rewards of such an elaborate process have not seemed worth while. On the other hand analysis of texture has been confirmed as important. More recently the resistance of the substratum to boring has been investigated by Chapman (1949) and Carruthers (1954), the technique being, so far, only practical intertidally and to a few feet below water level. In 1934 Day & Wilson showed that larval settlement is affected by partical size and this line of research has been taken much further by Wilson (e.g. 1953, *a*, *b*) who has shown the importance of the presence of organic matter, both living and dead. The amount of organic matter present is important for a variety of reasons summarized by Trask (1939) and Sverdrup, Johnson & Fleming (1942), but in the present context chiefly as food for the benthos. The importance of this is stressed by Davis (1925) amongst others for he thinks '. . . it not improbable that the association of various groups of animals with soils of particular texture is not so much influenced by the texture *per se* as by the food conditions of which the size of the soil particles is a correlated indication' (quoted from Jones 1950). It is axiomatic that the flora and fauna of the bottom in turn modify it, often profoundly. This has been clearly shown for muds by Moore (1931) although it is not so evident with sands and gravels. Moore also shows that several physical and chemical factors change progressively with increasing depth below the surface of the mud.

These notes refer to substratum texture and its content of dead organic matter both of which are undoubtedly very important features so far as the biota are concerned. Unfortunately workers in this field have been hampered by technical difficulties and comparison of their results is further complicated by differing methods of presentation. Experts in the many techniques of mechanical analysis,

organic analysis and in the statistical presentation of results are by no means agreed as to the best methods to be followed. Consequently it is not surprising that biologists have tried diverse methods and that the literature on substratum analysis is becoming more and more confusing. It has become apparent from the literature that there are dangers in adopting the techniques of other branches of science without modifying them to particular ecological needs. These notes are the result of the author having spent much time following procedures which turned out to be unsuitable for his particular requirements. They are presented particularly to newcomers in this field to provide something of a synopsis of recent work in an attempt to prevent similar waste of time. The problems of texture analysis and organic analysis are first discussed in regard to recent work, and then notes on analytical procedures are given, some proven methods being recommended and others which are controversial being suggested.

TEXTURE ANALYSIS

This is the determination of the relative quantities of particles of different sizes in a sample of the substratum. Most aspects of this analysis are admirably considered by Krumbein & Pettijohn (1938) and are summarized by various authors in Trask's symposium (1939*b*). The whole analysis involves pretreatment, mechanical analysis and presentation of results. Although each is a separate manipulation it is imperative that they be considered as a whole before collection of the sample.

(*a*) *Pretreatment*

All processes from the moment of collection until mechanical analysis come under this heading. The importance of pretreatment is often not realized and lack of foresight easily produces analyses which are invalid in regard to what they purport to express. Recently ecologists have tended to follow the practices of agricultural soil analysts without suitable modification. Agriculturalists appear to be interested in the analysis of the smallest particles which comprise the crumbs and clods which they find naturally. Consequently they destroy the agents such as organic and carbonaceous matter which bind the particles into larger aggregations. Carbonates are also removed because they give misleadingly high values to the silt and clay grades if finely divided. But surely marine animals are affected by the crumbs of the substratum as present around them and not by the component particles of the crumbs? Carbonates in the form of shell, bits of Polyzoa etc. and the compound crumbs form an integral part of the environment of a marine creature. Therefore, ecologists must not dissolve the shell nor break up these crumbs, for if they do so they create conditions which are abnormal to the creatures of the substratum. Although this was recognized in 1931 by Moore more recent work can be criticized in this respect.

In the case of particles less than about 0·05 mm in diameter, which are those below the range of most sieves, crumb sizes are affected by the phenomenon of aggregation, so that these small particles tend to clump together under influences

of ionization, hydration and mechanical agitation. The effect is well illustrated by the coagulation and subsequent deposition of river-borne silt when it meets the sea (Day 1951). For further details the reader is referred to Krumbein & Pettijohn (1938, p. 57ff.) and Gripenberg (1939). The effects of the factors influencing aggregation are reversible but the extent to which changes affect crumb aggregation or dis-aggregation cannot be calculated. If mechanical analysis of particles of sub-sieve size is desired it is important that pretreatment should not modify the degree of aggregation of the particles. In the absence of precise knowledge the only way to ensure that this remains unchanged is to collect the substratum sample with some of the water which naturally lies above it and to maintain this water at natural salinity, pH etc. This obviously precludes drying of the sample or treatment with formalin. In estuarine work particularly this raises great practical problems, and the most urgent need of hydrobiological substratum analysis is to determine what liberties may be taken with samples for the sake of convenience without significantly altering the degree of aggregation of the particles. Unfortunately time has not permitted the author to start this work.

(*b*) *Mechanical analysis*

It is unfortunate that particles of different sizes cannot be separated by the same means throughout their size range. Gripenberg (1939) mentions the following methods as best within the following size ranges: sieving—larger than 0·10 mm, elutriation—0·20-0·02 mm, sedimentation—smaller than 0·10 mm. Krumbein chooses 0·062 mm as the lowest limit for sieving (Krumbein & Pettijohn 1938) because suitable sieves are readily obtainable and this size is near the upper limit of applicability of Stokes's Law or Wadell's practical sedimentation formula whereby the smaller sizes are calculated. Moreover, this size is the lowest limit of sands in the Wentworth classification.

Sieving is the simplest way of separating medium-sized particles. For precise work the underlying principles of the method should be remembered (Krumbein & Pettijohn 1938). The most important point is that the sorting action of sieves is based on the least cross-sectional area of the particles and this area may or may not have a fixed relation to their volumes. This must be borne in mind when many of the particles are lath-shaped, e.g. shell, spines, spicules. Some workers prefer sieves with round holes but the majority use square-mesh sieves. The difference in results is probably only important in work of the most detailed sort. If sub-sieve particles are to be analysed then sieving must be done wet (see above), but if not then it is usually more conveniently done dry, often by machine. Krumbein notes that wet sieving is not as satisfactory as dry since 'it appears that the film of water in the wet sieve prevents some small particles from passing through'.

It has already been suggested that mechanical analysis of sub-sieve grades is not worth while if the pretreatment of the sample is suspect. Analysis may be of two kinds. Either the sample is subdivided into discrete grades which can be handled separately—methods which do this are elutriation and decantation; or the sample

is not actually subdivided but the constituent grades are determined by calculation—various sedimentation methods achieve this, e.g. pipette and hydrometer methods.

Elutriation was used by Borley (1923), Pirrie, Bruce & Moore (1932) and Fraser (1932). The accuracy of their apparatus is criticized by Beanland (1940), but she does not comment on the type of water used in their elutriators. Certainly in the first two cases it was fresh water whereas the sediments analysed occurred naturally beneath sea-water, but this criticism is important only where Borley's silt grades are concerned and these are noted to be third in order of abundance in his samples. Pirrie *et al.* state that particles smaller than 0·1 mm were negligible in all their samples, and larger particles are not significantly affected by agglomeration. Moore (1931) used an elutriator worked with sea-water to separate marine muds into four grades. These grades are not considered in terms of particle size, although current speeds in each chamber of the elutriator are given, for Moore notes a wide range in density of the particles which causes large, light particles and small, dense ones to collect in the same grade. The chief disadvantage of elutriation appears to be the rather elaborate apparatus required and this disadvantage is increased by the necessity to use 'natural water'. However, the method appears to be rapid and simple in manipulation.

Decantation was used by Allen (1899) and Smith (1932) to separate into two fractions the material passing a 0·5 mm sieve. Allen certainly used 'natural water' (sea-water) to suspend the sediment which was then allowed to settle for 1 minute before decantation; he notes that decantation was usually repeated once. Allen states the time for decantation but does not in fact stipulate the height of the suspension although it probably was standardized. It is noteworthy that Worth (in Allen 1899) comments that the 'fine sand' separated by this method was of very variable size and probably this was due, not to sedimentation from differing heights, but to the great variation possible in particles smaller than 0·5 mm (e.g. see Table 1). Later workers such as Rees (1940) and Holme (1949) also used decantation but followed agricultural practice and disaggregated their samples chemically, while Holme (1953, 1954) employed repeated decantation in distilled water to separate particles greater and smaller than 0·0313 mm. He mentions that pretreatment of the grades included first drying and then treatment with warm hydrogen peroxide. Objections to the methods of these recent workers can be made in respect of the factors discussed above under 'Pretreatment'.

Decantation is very slow for dispersed soils (Piper 1947). The fact that for ecological purposes, samples must be in 'natural water' might make the method more feasible because the particles would remain aggregated and so would settle comparatively rapidly.

In the category of sedimentation methods Beanland followed agricultural practice and used Robinson's pipette method (Robinson 1922) for calculating four grades from 0·2 to <0·002 mm by sedimentation after ammoniacal dispersion. Quicker methods are based on various hydrometer devices (Krumbein & Pettijohn 1938). The Bouyoucos Hydrometer method (Bouyoucos 1936, Piper 1947) is

widely used but would have to be modified as a consequence of using 'natural' water. If the separation of individual grades is not wanted, rapid hydrometer techniques could be developed for dispersions in waters of different salinities.

(*c*) *Presentation of results*

Both sieved and sub-sieve grades must be evaluated on the same basis even though obtained by different methods. This basis has usually been that of air-dried weight which contains an error in that the finest grades are hydrated more than the coarser due to the constitutional water of the clay particles. In addition grades contaminated with salt contain variable amounts of hygroscopic moisture. Both errors are avoided if results are expressed on an oven-dry basis as recommended by Piper (1947). Pirrie *et al.* (1932) evaluated their grades on the basis of drained, wet weight in the case of particles larger than 2 mm, and claim that the percentage composition so calculated corresponds to within 1% with that of samples evaluated by 'dry' (air dry?) weights. Unfortunately this simple procedure could not be applied to smaller particles without loss of accuracy and these they evaluated on a 'dried' basis, relating the coarse and fine material with a ratio. This method might be advantageous in saving time where many samples have to be analysed but has not been adopted in the model analysis suggested in this paper.

Fraser (1932) thought it would '. . . be of more value to express results as volumes, this not being dependent upon the specific gravities of the various materials and as it is volume that is the biological factor concerned'. Although gravels and sands were analysed by him on a volume basis he weighed the sub-sieve grades and the lack of uniformity is confusing. Measurement of volumes involves finicky manipulation and seldom approaches the accuracy of weighing (see Appendix). Although Fraser's contention seems perfectly true, the increased manipulation necessary and rather low accuracy obtained outweigh, in my opinion, the advantages of the method.

The presentation of the results of analysis in a comprehensible manner is another problem. One of the difficulties in understanding other workers' results is the variety of grade scales used (see Table 1). Usually the scales are arbitrary, with the diameters of successive sieves bearing no constant mathematical relationship to one another. Such were the different scales adopted by Allen (1899), followed by Borley (1923) and Smith (1932), Fraser (1932), Pirrie *et al.* (1932), Beanland (1940) and Holme (1949). However, Rees (1940) followed the logarithmic Atterburg scale of the agriculturalists, and Holme (1953, 1954) followed part of the Wentworth scale into which he inserted an extra grade. Conversion of these analyses to a common basis is virtually impossible. The concept of a grade scale is well discussed by Krumbein & Pettijohn (1938), and the value of a geometric scale, such as the Atterburg or Wentworth scales, is emphasized. In the Wentworth scale, which is adopted by practically all American sedimentary petrologists, the minimum diameters of grades are halved successively from 4 mm for 'pebbles' to 1/16 mm for 'very fine sand'. This scale gives more suitable gradation for

marine sediments than the Atterburg scale the gradation of which was found unsuitable by Holme (1949).

Some workers have expressed their results as the percentage of each grade related to the whole sample. Worth (in Allen 1899) attempted to obviate this cumbersome method by calculation of an 'average grade' for each sample and Borley's 'representative number' (1923) was an improvement. Recently Holme (1954) employed the 'arithmetic mean' which differs only slightly from Borley's

Table 1. *Comparison of the grade scales of some British ecologists with the Wentworth scale.*

Figures show minimum mesh sizes in mm, sieved grades above the horizontal lines. Round holes were used by Allen, Borley, Pirrie, Bruce & Moore, and Fraser down to and including 0·75 mm. Holme (1953, 1954) and Fraser below 0·75 mm used square mesh. The remainder give no note on mesh shape. It has not been possible to include the grades recognized by Moore (1931).

Allen (1899); Smith (1932)	Borley (1923)	Fraser (1932)	Pirrie, Bruce & Moore (1932)	Rees (1940)	Bean-land (1940)	Holme (1949)	Holme (1953, 1954)	Went-worth Scale
								64
		50						
		25						
15	15							
	10	10						
			6					
5	5	5						
		4·5						
		4	4					4
		3·5						
		3						
2·5	2·5	2·5			2·5			
		2	2	2		2	2	2
1·5	1·5	1·5			1·5			
1	1	1	1		1		1	1
		0·75						
0·5	0·5	0·5	0·5		0·5	0·5	0·5	0·5
		0·35						
			0·25			0·256	0·25	0·25
	0·2			0·2	0·2	0·22	0·21	
		0·15						
							0·125	0·125
?0·1	0·1	0·1	0·1					
		0·06						0·062
	0·05							
					0·04			
							0·031	
		0·02		0·02		0·02		
					0·01			
								0·004
				0·002	0·002			

'R.N.'. All are indices attempting to express by one figure the chief characteristics of the sample. Holme notes one drawback of the arithmetic mean which is '. . . more affected by changes in the percentages in the coarser grades than in the finer', and this comment applies also to Borley's 'R.N.'. This drawback is particularly unfortunate since small differences in silt content may be very important, as was shown by Holme (1949, p. 228; difference of 4%). The above methods are, like histograms, based on the assumption of discrete size grades with the inherent drawbacks of the assumption (see Krumbein & Pettijohn 1938). The same data can be

used to construct cumulative curves representing continuous frequency distribution as has been done by Holme (1953, 1954). The cumulative curve shows for any given particle size the percentage of the substratum which consists of particles greater or smaller than that size. Such cumulative curves are used by agriculturalists (Robinson 1922, Piper 1947) and in many studies of marine sediments (Sverdrup *et al.* 1942). These curves reduce the necessity for qualitative description of the sample for they yield several numerical values which serve descriptively. A detail in which the European agriculturalists and the Americans differ is that the former place particles of smallest size to the left of the figure whereas the latter place them to the right (see Krumbein & Pettijohn 1938). Holme (1953, 1954) follows the American practice.

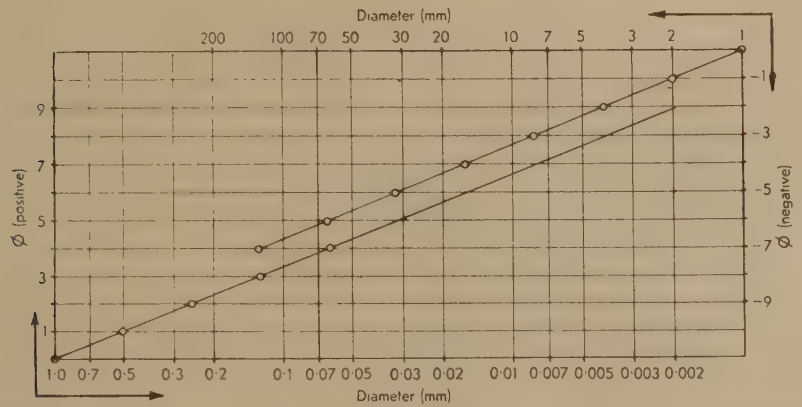


Fig. 1. Chart for conversion of Phi values into corresponding particle diameters in millimetres. The lower line applies to the bottom and left-hand scales. (Based on Krumbein.)

Krumbein emphasizes the importance of selecting convenient mathematical methods for the simplification of statistical treatment. A variety of methods based on cumulative curves are available and of these the Phi (Φ) scale offers an attractive method. Phi substitutes a logarithm for particle diameter in millimetres and so translates the arithmetically unequal class intervals of the Wentworth scale into equal intervals. Thus the cumulative curve of an analysis can be plotted on squared graph paper instead of semi-logarithmic without changing the shape of the curve. The median (Md_ϕ), or the value on the x-axis corresponding to the 50% value on the y-axis, is read in Phi terms and translated into the corresponding diameter in millimetres by use of a conversion chart (Fig. 1). Half the substratum is composed of particles smaller than the median diameter and half of larger particles. The median diameter is most graphically expressed in microns rather than in fractions of a millimetre.

Because of the possibility of sampling errors at the upper and lower particle size limits the cumulative curves are usually only analysed between the first and third quartiles. Two statistical measures based on quartile values are commonly used.

A measure of the slope of the curve is the Phi quartile deviation (QD_φ) which may be expressed:

$$QD_\varphi = \frac{Q3_\varphi - Q1_\varphi}{2}$$

where $Q3_\varphi$ and $Q1_\varphi$ are the values of Phi for the third and first quartiles. The slope of the curve indicates the sorting efficiency of the sedimentary agencies. Perfect sorting would be represented by a vertical curve and a QD_φ value of zero. Double the Phi quartile deviation indicates the number of Wentworth grades between the first and third quartiles or, in other words, the size-spread of the middle 50% of the sample.

Whether the curve is straight or curved between the quartiles is indicated by the Phi quartile skewness (Skq_φ).

$$Skq_\varphi = \frac{Q3_\varphi + Q1_\varphi - 2Md_\varphi}{2}$$

A straight line between the quartiles has $Skq_\varphi = 0$. Negative values indicate that the mean of the quartile values is to the left of the median value: in other words that the smaller particles are better sorted than the larger.

The arithmetic involved in calculating the Phi quartile deviation and Phi quartile skewness is simpler than that for corresponding measures based on curves constructed without use of the Phi scale.

To recapitulate: the construction of cumulative curves with use of the Phi scale involves no more work than that in calculating Worth's 'average grade' or Borley's 'representative number' or Holme's 'arithmetic mean' but avoids the drawbacks from which they suffer. In addition several figures are readily obtained from the graph instead of the single index of Worth, Borley or Holme and these figures are more descriptive of the substratum, having geometric significance in terms of particle size on the Wentworth scale and being readily visualized in terms of the sedimentary curve.

As an example of this method of presentation the cumulative curves of three marine sediments are shown in Fig. 2. If the curves are examined in the light of their medians, quartile deviation and quartile skewness the following points are apparent:

(i) FAL. 283, with a median of −0·55 Phi, is a much coarser substratum than either of the others whose medians lie at 2·55 and 3·60 Phi. The Wentworth grade corresponding to the median of FAL. 283 is 'very coarse sand' whereas the medians of FAL. 94 and LIZ. 23 indicate 'fine sand' and 'very fine sand' respectively.

(ii) The Phi quartile deviation of FAL. 94 is 0·3 which is near zero and so indicates a very much better sorted substratum than FAL. 283 and LIZ. 23 with quartile deviations of 1·45 and 1·65 respectively. The data may be visualized better if the quartile spread of the sample is considered. This value is twice that of the quartile deviation and indicates the number of Wentworth grades into which the median half of the sample falls. Thus the median half of FAL. 94 falls into 0·6 grades by this reckoning; the curve in Fig. 2 shows that actually 75% is retained by the 0·125

mm sieve. In the case of FAL. 283 the quartile spread is 2·9 which means that the median half of the sample is spread over 2·9 Wentworth grades or is contained in three sieves of the series. LIZ. 23 has a quartile spread of 3·3 and so is rather worse sorted than FAL. 283.

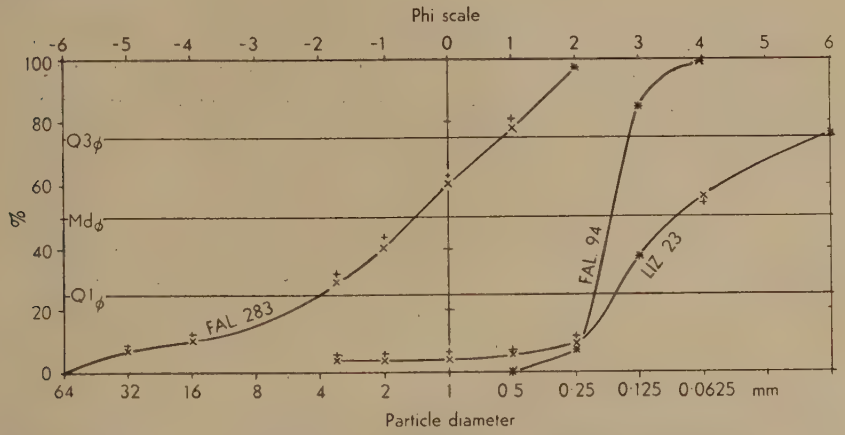


Fig. 2. Cumulative curves of three marine sediments plotted against the Phi scale. Cumulative curves by weight are drawn and the positions of cumulative curves by volume are indicated by plus signs.

The lowest scale of figures gives the equivalent diameters in millimetres for Phi = −6 to+4. Nomenclature of the grades according to the Wentworth scale is as follows:

64 - 4	mm	Pebble.	0·25 -0·125	mm	Fine sand.
4 - 2	,,	Granule.	0·125 -0·0625	,,	Very fine sand.
2 - 1	,,	Very coarse sand.	0·0625-0·0039	,,	Silt.
1 -0·5	,,	Coarse sand.	<0·0039	,,	Clay.
0·5-0·25	,,	Medium sand.			

(iii) The curve for LIZ. 23 is definitely skewed, having a Phi quartile skewness of 0·6. Being positive this value indicates that the particles larger than the median are better sorted than smaller ones. The Phi quartile skewness for FAL. 94 and FAL. 283 is 0 and −0·15 respectively, showing that in both samples the efficiency of sorting of the larger and of the smaller particles was of the same order. It should, however, be noted that the skewness of LIZ. 23 may be due to the different methods of mechanical analysis for particles greater than 0·066 mm (sieving) and for those smaller (hydrometer method).

The field notes on these samples were: FAL. 283 a coarse, shelly sand; FAL. 94 a clean, fine sand with ripple marks; and LIZ. 23 a rather clayey mud. The full curves accord well with these field descriptions. The presence in LIZ. 23 of 'granules' is due to dead pelecypod shells which presumably derived from animals that grew and died in the mud; therefore, they cannot reflect the sorting action of the overlying water.

It would be possible to evolve statistical measures corresponding to the quartile deviation and quartile skewness but based on the first and ninth deciles. In that case 80% instead of 50% of the sample would be considered. The validity of this would depend on the efficiency of sampling of the largest and smallest particles of a sample: most samplers tend to miss the largest or to lose some of the smallest.

When deciles are to be considered the necessity for sub-sieve analysis increases for it is required if as much as 10% of the sample passes the finest sieve.

ORGANIC ANALYSIS

As considered in this paper the object of this is to determine the amount of dead organic matter available for food purposes, although similar analysis might serve organic pollution problems. Analysis could be made on a whole substratum sample but more interesting results accrue if the component grades are analysed separately. Hence analysis for organic matter must follow texture analysis. Trask (1939*a*) writes that 'the quantity of organic matter in sediments is determined indirectly, usually by multiplying by an appropriate factor, some property of the sediment that is related to the organic content—such as the content of carbon, nitrogen, phosphate, or volatile substances'. Technical difficulties are considerable. Thus Pirrie *et al.* (1932) considered, and abandoned as inadequate, various methods of estimation including that of loss in weight on ignition which is complicated by the presence of carbonates (shell) and soil colloids. This method of estimation was used by Beanland (1940) after removal of carbonates by acid, but her results still include loss of constitutional water of the colloids which must have been abundant in the muds met with. Sverdrup *et al.* (1942) state that oxidation either by ignition or by 'wet combustion' is difficult and time consuming and that the organic content is commonly obtained indirectly by estimation of nitrogen.

Various methods of analysis for agricultural purposes are discussed by Piper (1947) and three are described in detail. Of these the Walkley & Black method of wet-oxidation by hot chromic acid followed by titration offers a rapid and not very expensive technique which is apparently the only wet-oxidation technique approved by the International Society of Soil Science. Piper gives full details of the method in its (then) latest form. The method estimates the percentage of carbon of organic matter excluding carbonates. It is unaffected by elementary carbon and nitrates only interfere if present in amounts in excess of one-twentieth of the carbon content. Perhaps the most attractive feature is that interference by chlorides can be suitably corrected. Piper quotes that '. . . Walkley finds that the percentage recovery . . . varies from 60% for some subsoils to 90% or more for peat soils, taking values obtained by dry combustion as the standard of comparison. For the majority of agricultural surface soils the mean recovery lies between 75% and 80%'.

There is a definite indication that the results of Walkley & Black analyses of marine soils must be treated with reserve. In a test forty-three different grades of seven different substratum samples were analysed (see Table 2) after the composition of each grade had been observed microscopically. The great majority of grades were more than half composed of shell of various kinds, Polyzoa fragments and spicules. No grades gave Walkley & Black values below 0·04% (which occurred in FAL. 217) and thirty-three analyses gave values from this figure up to 0·4% although visually they were all noted as 'free of organic matter'. The organic carbon deter-

mined was that of the dead shell, etc. which cannot be regarded as available for use as food. The remaining ten grades had values from 1·1% to 4.6% and half of these were the grades of one substratum sample (FAL. 237) which was composed almost entirely of faecal pellets. Although the Walkley & Black values for the faecal pellets were so high it was problematical how much of this carbon was available as food, for it had already passed through the gut of some animal. Microscopic observation of each sample noted that organic matter, appearing as 'fluff', was confined to the finest grades, particularly to the sub-sieve grade (smaller than 0·066 mm) and in general this contention was confirmed by the analyses. Apart from the sample composed of faecal pellets, only one sieved grade (in FAL. 222) had a high value.

Table 2. *Percentages of organic carbon (Walkley & Black values) of the grades comprising various substratum samples. For each sample percentages have been calculated for the total 'available' carbon and for the total 'available' organic matter present in the sample* (see p. 384).

Samples Field description	FAL. 94 Clean, fine sand.	FAL. 283 Shelly, very coarse sand.	FAL. 217 Shelly, medium sand.	FAL. 222 Shelly, coarse sand.	FAL. 228 Shelly, coarse sand & khaki mud.	FAL. 237 Green, faecal-pellet mud.	LIZ. 23 Sticky, greyish mud.
Depth (m)	2-3	14	18	40	64	78	38
Minimum particle diameter (mm)							
32	.	0·4	.	0·2	.	.	.
16	.	0·3	0·4	0·2	.	.	.
8	.	0·4	0·2	.	.	.	.
4	.			—	0·1	.	—
2	.	0·3	0·2	0·3		.	—
1	.	0·3	0·2	—	0·2	.	—
0·5	0·4	0·3	0·0	0·1	0·3	1·5	—
0·25	0·2	0·2	0·1	—	0·3	4·4	—
0·125	0·4	0·3	0·1	0·1	0·3	4·6	0·1
0·066	0·1		0·1	1·1	0·3	2·8	0·3
<0·066	1·6			3·7	1·6	3·4	1·4
'Available' organic carbon	0·004	0·000	0·000	0·031	0·144	3·20	0·433
'Available' organic matter	0·010	0·000	0·000	0·074	0·346	7·73	1·039

— Grades not analysed.

To convert the percentage of carbon to the percentage of organic matter a factor must be used, which depends on the chemical composition of the organic matter. This is discussed by Trask (1939*a*), Sverdrup *et al.* (1942) and Piper (1947), and factors from 1·67 to 2·0 have been suggested. Trask recommends 1·8 which corresponds with a carbon content of 56%.

NOTES ON ANALYTICAL PROCEDURES

This section is intended as a guide to procedures of analysis of sediment texture and organic content and to presentation of the results of these analyses. It would have been helpful to present step by step schemes for each analysis but this has

not seemed worth while for reasons which will be given below. Full procedural details are only given for organic analysis where one method has appeared to be far more suitable than others. This method has been extracted from a book and the text is left in its original form. In the case of mechanical analysis of coarse sediments the methods adopted depend upon whether analysis of particles of sub-sieve size will also be attempted, and whether organic analysis is contemplated. Procedures for mechanical analysis by sieving are so well known that it would be pointless to give step by step instructions covering the variations that might be required when a few comments suffice. The third type of analysis considered here, that of mechanical analysis of particles of sub-sieve size, is the most controversial. A great number of methods are possible with many variations of detail and no single method is pre-eminently suitable. Furthermore no method has been fully investigated with regard to its accuracy when the sediment is dispersed in natural water. In such circumstances a detailed procedure cannot reasonably be recommended.

It is assumed that samples are truly representative of the substratum. In the case of sands and muds a suitable quantity for field collection is 450 ml (the volume of a 1 lb preserve jar) but this quantity should be doubled for gravels. It must be decided at the time of field collection whether analysis of sub-sieve grades is to be attempted or not because if it is desired then the sample must be collected with some natural water. As shown earlier, sub-sieve analysis is usually only necessary if more than 25% of the sample passes the finest sieve. With most gravels and sands sub-sieve analysis is probably unimportant owing to the small quantity of silt present. With muds such analysis seems unavoidable despite the difficulties involved.

All sieves used should conform to the Wentworth grade scale (see Fig. 2) with minimum mesh size of 0·062 mm. It should be noted that the Phi scale can be used even if the Wentworth grade scale is not adhered to, since any mesh-size has a corresponding Phi value. This is convenient if one or two of the sieves available do not fit the Wentworth series, but if none of the sieves fit then the graphic value of the Phi quartile deviation and Phi quartile skewness is greatly diminished. British Standard sieves of mesh 5, 8, 16, 30, 60, 120, and 240 fit the scale reasonably from 4 to 0·0625 mm, but the first and last sieves, which have mesh sizes of 3·353 mm and 0·066 mm, must be given Phi values of $-1{\cdot}75$ and $+3{\cdot}9$ respectively as can be calculated from Fig. 1.

(*a*) *Analysis of gravels and sands*

It is presumed that with most gravels and sands sub-sieve analysis is not desired and in these cases samples may be treated with preservative for the animals they contain or the animals may be removed and the samples put into bags and air dried. An aliquot is taken for grade analysis, about 150 ml being sufficient with sieves of 20 cm diameter; a larger sample is unwieldy and reduces sieving efficiency.

Salt should be leached-out before analysis since its weight is otherwise added to

that of the grades. There are two further possible reasons for salt removal: its hygroscopic properties would interfere with the separation of fine particles if dry sieving were proposed, and if organic analysis were to be done on the grades then they should either be free of salt or their salt content known. Leaching and sieving are combined if samples be wet-sieved under fresh water. Animals in the preserved samples can be removed at this stage. Care must be taken that fines passing the finest sieve be not lost for their weight must be known. The separated grades should finally be washed with a jet of fresh water. Probably dried samples could be leached by immersing the bags in changes of fresh water but the author has no experience of this. The samples could then be dried again and sieving done in a nest of sieves on an automatic shaking machine. This procedure might be the easiest if a great number of substrata were to be analysed.

All grades should be oven-dried at 105° C. and evaluated on the basis of oven-dry weight.

The results of mechanical analysis may be tabulated as follows:

Weights (g)		Cumulative percentage	Phi value equivalent to sieve mesh size
Weight retained by 4 mm sieve	g_1	$g_1 \times 100/G$	−2
Weight retained by 2 mm sieve	g_2	$(g_1+g_2) \times 100/G$	−1
Weight retained by 1 mm sieve	g_3	$(g_1+g_2+g_3) \times 100/G$	0
Weight retained by 0·5 mm sieve	g_4	$G \times 100/G$	1
Weight of sample	G		

The cumulative percentages are graphed against Phi and so a cumulative curve, such as those of Fig. 2, is quickly constructed.

From the cumulative curve of each sample the following should be calculated and presented: the median diameter in microns, the Phi quartile deviation, and the Phi quartile skewness (see pp. 373-4); comments on the curve should be made, particularly regarding its extremes and any points of inflection.

(*b*) *Analysis of muds*

If analysis of sub-sieve particle sizes is desired a laborious procedure seems inevitable. As has been mentioned research is very necessary to determine what liberties may be taken without affecting the agglomeration of the sub-sieve particles but which will simplify pretreatment and analysis. The notes below may prove to be over-cautious: it is to be hoped that they stimulate detailed investigations.

The sample is retained with a little natural water in an air-tight jar. No preservative may be added and so animals must be removed before decomposition starts, this being especially important if analysis for organic matter is subsequently to be made. A water sample must be simultaneously taken for determination of salinity and pH.

The aliquot of 150 ml is passed through successively finer sieves under 'natural water'. Probably natural water can be replaced without great resulting error by fresh or sea water which has been adjusted to correct salinity and pH. About 2 l. should be sufficient for the complete analysis unless an elutriometer is used. The separated grades are then washed free of salt with tap water, this having negligible effect on the aggregation of particles as large as those retained by sieves. The grades are transferred to weighed dishes, oven-dried at 105° C, and weighed; the oven-dry weight of each grade can thus be calculated. Flat and round-bottomed porcelain dishes 9-13 cm in diameter are suitable, and weighing is greatly speeded if their empty weights (to the first decimal place) are scratched on with a diamond. Weighing should, however, be accurate to the second decimal.

It is necessary to know the oven-dry weight of the fines which pass the 0·062 mm sieve in order to determine the weight of the whole aliquot. As this cannot be done before sub-sieve analysis, care must be taken not to lose any in the process. Three methods of sub-sieve analysis are tentatively suggested:

(i) Elutriation with artificial 'natural' water (see above) continuously circulated through a filter; this method effects subdivision into several grades.

(ii) Separation into two grades can be done fairly simply by decantation if no great accuracy is required. The suspension is thoroughly mixed in a 1 or 2 l. measuring cylinder and allowed to settle. At a known time-interval the liquid is divided into two at a known depth by drawing-off the upper layer with an upturned siphon or by means of a built-in tap. To effect complete separation by this method is tedious because the lower portion of the suspension contains particles smaller than those at the level of separation and therefore it must be diluted to original volume and the separation repeated. Probably two repetitions would be accurate enough for most purposes.

(iii) The gradation may be calculated from hydrometer readings without the grades actually being separated. The author used the following simple procedure but the results require confirmation as to their accuracy. The sub-sieve fines in the sieving water were concentrated by prolonged standing and removal of clear water. They were transferred to a 1 or 2 l. measuring cylinder with the aid of a wash-bottle containing 'natural water' and their volume noted. They were thoroughly mixed by means of a perforated plunger (Piper 1947, p. 65 'stirring paddle') and the time at which stirring ceased was noted as 'zero' time. A hydrometer was gently inserted and readings of the top of the meniscus taken as soon as possible and then roughly every 2 min at noted times, the instrument being left in the suspension. The bottom of the meniscus could not be read because of excessive turbidity. The hydrometer used was of glass, reading 1000-1050, bulb about 12 cm long and stem about 11 cm long. After about 30 min the reading was almost constant and the temperature of the suspension was noted. The salinity of the 'natural water' used was noted. The method of calculating results is given below.

After sub-sieve analysis by any of the above three methods the weight and volume of the dry grades must be determined so that the full weight of the sample

is known and so that the density of the sub-sieve grades can be calculated. The grades are concentrated by standing overnight under covers to avoid evaporation, and the clear water is drawn off. Some loss of colloids is usual, but with care the weight lost is negligible compared to that of the whole aliquot. Each grade is transferred to as small a weighed measuring flask as possible and the volume made up to the mark with natural water. The whole is weighed and so both the combined weight and combined volume of grade and water is calculable. The contents are shaken and poured without loss into a large, weighed evaporating dish. A round-bottomed dish of 15 cm diameter is about the smallest that can be used. The flask is cleaned with *distilled* water which is added to the dish. The dish and contents are oven-dried at a 105° C to constant weight and the weight noted. The difference between the oven-dry weight of the grade plus salt and the weight of the grade plus natural water in the measuring flask gives the volume of water present in the flask and so the volume of the grade is found by difference. Since the salinity of the natural water is known the weight of salt present in the dry grade is known and subtraction gives the oven-dry weight of the grade alone. The approximate density of the grade can be calculated, the figure not being very accurate because of the crudeness of the volume determination.

Holme (1954) speeds sedimentation by flocculating the particles with a little alum solution and a few drops of acetic acid, later filtering the suspension through a weighed filter paper and then washing out the contaminants. A method based on this might be preferred to that outlined in the above paragraph.

The calculation of the particle sizes determined by an elutriometer is largely dependent on the apparatus and so cannot be discussed here; the oven-dry weights of the grades are directly determined as above. In the decantation method the size corresponding to that of the particles at the level of division is calculated by means of Stokes' Law; this is more conveniently described under the hydrometer method below. Decantation is probably the simplest method for determining the position of the third quartile if no more than this is required. In the hydrometer method used by the author the readings were converted to bottom-of-the-meniscus readings by applying a correction for its estimated height and these readings were graphed against time from 'zero'.

Results were calculated by substitution in the equation of Stokes' Law (Piper 1947):

$$v = \tfrac{2}{9} \times g r (D - d)/\eta$$

where (all in c.g.s. units)

v = velocity of sedimentation
g = acceleration due to gravity
r = radius of the spherical particles
η = coefficient of viscosity of the fluid
D = density of the spherical particle
d = density of the fluid.

For any time (t sec) the corresponding hydrometer reading was read from the graph. The effective depth of the hydrometer was the height (h cm) from the centre of flotation (marked by a dot on the bulb) to the stem reading at the bottom of the meniscus:

$$h/t = v.$$

Sverdrup *et al.* (1942, p. 69) give a short table of the viscosity of pure and saline waters at 5° intervals from 0-30° C. The table is 'after Dorsey (1940)' whose book I have not seen but possibly it contains a fuller table. Salinity has a small effect on viscosity but temperature a large effect. The figures are in $\mu \times 10^3$ c.g.s. units andc onsequently have to be divided by 10^3 for substitution in Stokes' Law above.

The density (D) of the particles was determined directly as described above. The density (d) of the fluid was calculated from its salinity and temperature with the aid of Knudsen's Tables (1901) where:

$$d = (\sigma_t/1000)+1.$$

Sverdrup *et al.* (1942, p. 57) state that tables for computing σ_t directly from temperature and salinity have been prepared by two separate workers.

For each sample Stokes's Law was rearranged in the form $r=\sqrt{hK/t}$, where the constant $K = 9\eta/2g(D-d)$ and for any given time (t) the diameter of the particles at the effective depth of the hydrometer (h) = $20\,r$ mm.

The hydrometer reading (x_o) corresponding to that of zero time was obtained from the graph by extrapolation; this reading corresponded to 100% of the fines in suspension. The final hydrometer reading (x_f) when all fines were settled was similarly found. Then $x_o - x_f = 100\%$ of fines in suspension, and each hydrometer-unit $= 100/(x_o - x_f)\%$ of fines in suspension. Therefore, at any time (t), and corresponding hydrometer reading (x_t), the percentage of fines which had dropped below the effective depth of the hydrometer $= (x_o - x_t)100/(x_o - x_f)$. For each time ($t$) at which particle sizes had been calculated the weight of the particles fallen below the hydrometer was also calculated. It should be noted that this includes some of the finest particles.

All grades are evaluated on the basis of oven-dry weight and cumulative percentages are calculated as described above (p. 379) and plotted against corresponding Phi values. In the case of the sub-sieve grades equivalent Phi values are obtained from Fig. 1. The same results should be presented as suggested at the end of the sub-section dealing with the analysis of gravels and sands (see p. 379).

(*c*) *Organic analysis*

For estimation of organic carbon content by the Walkley & Black method aliquots of about 2 g are taken, finely ground in a mortar and then oven-dried at 105° C on watch glasses; afterwards they are cooled in a desiccator.

The following details of analysis are extracted from Piper (1947), by kind permission of the author, with some slight modifications and additions.

REAGENTS N Potassium dichromate: dissolve 49·4 g of $K_2Cr_2O_7$ (analytical reagent grade) in distilled water and dilute to 1 litre.

Sulphuric acid: not less than 96%.

Phosphoric acid: 85%.

Diphenylamine: dissolve 0·5 g diphenylamine in a mixture of 100 ml conc. sulphuric acid and 20 ml of water.

N Ferrous sulphate: dissolve 278·0 g of $FeSO_4 \cdot 7H_2O$ (analytical reagent grade) in distilled water, add 15 ml of conc. sulphuric acid and dilute to 1 litre. Standardize by titrating against 10·5 ml of N potassium dichromate, as described in the method given below. The ferrous sulphate is quite stable if kept under an atmosphere of hydrogen in the reservoir bottle of an automatic burette. A very convenient arrangement, using a burette with an automatic zero, is figured by Piper (1947, p. 225).

METHOD Piper recommends transferring each accurately weighed-out sample to a 500 ml Erlenmeyer flask, but a simpler procedure is to weigh-out each sample into a 15 cm round-bottomed porcelain dish. Calculation is simplified if the assay be made on samples which weigh in multiples of 0·3 g. Samples of 1·2 g are suitable for non-salty grades which appear to be free of organic matter and 0·6 g of salty grades or those rich in organic matter.

Add 10 ml of N potassium dichromate followed by 20 ml of conc. sulphuric acid. Where large numbers of analyses have to be carried out the dichromate is most conveniently added from a burette with an automatic zero and the sulphuric acid from an automatic pipette. In very shelly grades the addition of sulphuric acid must be cautiously made. Not more than about 1 ml should be added initially and the dish should be rocked until the effervescence dies down. The remainder of the acid can usually be added rapidly. The dish is placed on an asbestos sheet and stirred for a minute with a thin glass rod, then left to stand for about 30 min.

Add about 200 ml of water, 10 ml of phosphoric acid and 1 ml of diphenylamine indicator solution. Titrate by adding ferrous sulphate from the burette until the solution is purple or blue. Continue to add the ferrous sulphate in small lots of about 0·5 ml until the colour flashes to green. Then add 0·5 ml of N potassium dichromate to restore an excess of dichromate and complete the titration by adding ferrous sulphate drop by drop until the last trace of blue colour disappears. If more than 8 ml of the 10 ml of potassium dichromate originally taken have been reduced during the digestion, repeat the determination using a smaller sample. The blue colour frequently does not reappear on the addition of 0·5 ml of excess potassium dichromate but it soon redevelops after the addition of ferrous sulphate.

Large amounts of calcium sulphate (precipitated from calcareous soils) or silver chloride (if silver sulphate is used to prevent chlorine interference in saline soils — see below) tend to alter the shades of the colours produced. The colour change at the end point, however, is still quite sharp and easily recognized. Where chlorides are present in amounts not in excess of the molecular equivalent of carbon, 1·25 g of silver sulphate should be dissolved in each 100 ml of conc. sulphuric acid; 20 ml of this acid then contain sufficient silver to precipitate the whole of the chlorides as silver chloride and so prevent their oxidation by the chromic acid.

CALCULATION 1 ml of the N potassium dichromate is equivalent to 3 mg of carbon. The amount of carbon oxidized, expressed as a percentage of the sample, is therefore given by the expression:

$$(V_1 - V_2)/W \times 0{\cdot}003 \times 100$$

where V_1 = volume of N potassium dichromate (10·5 ml),

V_2 = volume of N ferrous sulphate in ml,

W = weight of sample.

V_2 is obtained by slide rule according to the concentration of the sulphate as determined by the standardization.

If the sample contained chlorides and the silver sulphate modification was not used, then the chlorides would be oxidized by the chromic acid with the liberation of free chlorine. A correction must be made for the chromic acid used in this way by deducting one-twelfth of the percentage of chlorine present from the organic carbon value calculated above; 11·83 g of chlorine are equal in reducing power to 1 g of carbon.

The results of the analyses can be corrected for three reasons. Firstly, they should be modified to represent more truly the organic carbon 'available' as food (see p. 377). It is suggested that all values of 0·4% and less be disregarded and that 0·4% be subtracted from higher values where the grades are composed of shell or faecal pellets. The resulting percentages would be those for 'available' organic carbon (e.g. Table 2). Secondly, a correction can be made because the Walkley & Black method does not effect full recovery of organic carbon (see p. 376). If it is assumed that recovery is 75% then the figures obtained by the Walkley & Black method must be multiplied by a factor of 1·3 to give percentages of 'available' organic carbon present in the sample. Thirdly, a correction can be applied to convert values for organic carbon into those for organic matter (see p. 377). Let Trask's factor of 1·8 be adopted. The second and third corrections can be combined in one factor, 2·4, by which the percentage of 'available' organic carbon, Walkley & Black value, is multiplied to estimate the percentage of 'available' organic matter present in the sample.

Thus, the following values may be presented according to requirements:

'Percentage of organic carbon, Walkley & Black value'.
'Percentage of available organic carbon, Walkley & Black value.'
'Percentage of available organic carbon present in the sample.'
'Percentage of available organic matter present in the sample.'

The definition of 'available' must be clearly stated and any factors used, given.

ACKNOWLEDGMENTS

I take great pleasure in thanking Professor J. H. Day for his invaluable advice at all times. In addition Mr B. A. Kantey, of the Department of Civil Engineering, has been kind enough to comment on the manuscript. Mr C. S. Piper and his publishers have contributed to the completeness of this paper by very kindly permitting me to quote extensively from an analytical procedure set out in his book (Piper 1947).

SUMMARY

1. Some features of soft substrata which affect the benthos are noted and it is suggested that two of them, namely texture and content of dead organic matter, are both important and amenable to study.

2. Recent work in this field by ecologists is reviewed and the desirability for uniformity in methods and presentation of results is stressed.

3. Some ecological work is criticized on the grounds that the methods of analysis have altered the natural state of the substratum. In texture analysis pretreatment, mechanical analysis and presentation of results must be considered together before actual collection of the sample.

4. The following suggestions are made:

(i) If sub-sieve analysis is to be attempted samples must be kept in 'natural water' before and throughout mechanical analysis, so that the degree of agglomeration of the fine particles is not altered.

(ii) Neither carbonates nor organic matter may be eliminated before mechanical analysis.

(iii) Sieves must conform to the Wentworth scale, the minimum mesh being 0·062 mm.

(iv) Grades should be evaluated on the basis of oven-dry weight.

(v) Results should be translated into cumulative curves related to the Phi scale, and the following given:

median diameter in microns; Phi quartile deviation; Phi quartile skewness; notes on special features of the curves.

5. Notes are given on procedures of mechanical analysis.

6. Methods of organic analysis are very briefly reviewed and the Walkley & Black method for estimation of organic carbon is put forward as suitable.

7. Corrections must be made to the Walkley & Black values to approach more nearly the figure for organic carbon available as food. Also the factor of 2·4 is suggested for converting the percentage of available carbon (Walkley & Black value) into percentage of available organic matter in the sample.

APPENDIX

Seven substratum samples were analysed and the grades evaluated both on a by-weight and by-volume basis. The object was to determine whether there were important differences in the results. The method of analysis was as follows. An aliquot was wet-sieved in natural water. The separated grades were washed free of salt in tap water and transferred to measuring cylinders of the minimum size compatible with the diameter of the particles and the quantity of the grade. In general the capacity of the cylinder was two to three times as great as the apparent volume of the grade. The combined volume of grade plus water was read and both transferred without loss into a weighed dish. The weight of grade plus water was noted, the whole oven-dried at 105° C and then reweighed. Loss in weight on drying gave (approximately) the original amount of water present, and since the combined volume of grade and water had been measured the volume of the oven-dry grade could be calculated. In the case of sub-sieve grades the

water used was saline and so the oven-dried grades contained weights of salt which could be calculated from the known salinity of the water. Thus the weight of each grade alone could be calculated.

The weight of each grade was accurate to the second decimal place $\pm 0{\cdot}01$. The volumes as read from the cylinders, were probably accurate to the first decimal $\pm 0{\cdot}1$ where the grades were less than 20 ml; and to the nearest whole number in larger grades. The method of volume determination was fairly susceptible to errors of manipulation but was preferred to that of adding water to the dry grade (adopted by Fraser 1932) because the grade ended up dry and ready for organic analysis. In check of accuracy, however, two dry grades were reconstituted with the weight of water lost on oven-drying and the combined volume agreed with that originally determined within the margin of error mentioned.

For each substratum cumulative percentages by weight and by volume were calculated and graphed against the Phi scale. The values of three of the substrata are entered in Fig. 2 where curves are only drawn for the by-weight values. In all seven samples the by-weight and by-volume curves were very similar. In two substrata they were effectively identical (including FAL. 94) and in the other five varied differently with each, in some running parallel (e.g. FAL. 283) and in others crossing (e.g. LIZ. 23) or diverging. But the maximum divergence of the cumulative percentages by weight and by volume at any particle size was 2·6% (FAL. 283, see Fig. 2). In comparing the results of analysis the by-weight and by-volume figures correspond as follows:

Median diameter	$\pm$ 25μ
Phi Quartile Deviation	$\pm$ 0·05
Phi Quartile Skewness	$\pm$ 0·1.

The following conclusions were drawn from this small experiment: analysis by volume is more laborious and less accurate than analysis by weight; in view of the low accuracy of analysis by volume the small differences in the by-weight and by-volume cumulative curves are not held to be important; in view of the above comments analysis is best done on the basis of weight.

REFERENCES

Allen, E. J. (**1899**). On the fauna and bottom-deposits near the thirty fathom line from the Eddystone Grounds to Start Point. *J. Mar. Biol. Ass. U.K.* (N.S.) **5,** 365-542.

Beanland, F. L. (**1940**). Sand and mud communities in the Dovey estuary. *J. Mar. Biol. Ass. U.K.* **24,** 589-611.

Borley, J. O. (**1923**). The marine deposits of the southern North Sea. *Fish Invest.* (II) **4,** No. 6.

Bouyoucos, G. J. (**1936**). Directions for making mechanical analyses of soils by the hydrometer method. *Soil. Sci.* **42,** 225-30.

Carruthers, J. N. (**1954**). A Penetrometer for use on water-covered beaches. *J. Mar. Biol. Ass. U.K.* **33,** 637-44.

Chapman, O. (**1949**). The thixotropy and dilatancy of a marine soil. *J. Mar. Biol. Ass. U.K.* **28,** 123-40.

Day, J. H. (**1951**). The ecology of South African estuaries. Part I. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Afr.* **33,** 53-91.

Day, J. H. & Wilson, D. P. (**1934**). On the relation of the substratum to the metamorphosis of *Scolecolepis fuliginosa* (Claparède). *J. Mar. Biol. Ass. U.K.* **19,** 655-62.

Davis, F. M. (**1925**). Quantitative studies on the fauna of the sea bottom. No. 2. Results of the investigations in the southern North Sea. *Fish. Invest.* (II) **8,** No. 4.

Dorsey, N. E. (**1940**). *Properties of ordinary water-substance.* New York.

Fraser, J. H. (**1932**). Observations on the fauna and constituents of an estuarine mud in a polluted area. *J. Mar. Biol. Ass. U.K.* **18,** 69-85.

Gripenberg, S. (**1939**). Mechanical analysis, pp. 532-57, in **Trask, P.D.** (ed.) (**1939b**).

Holme, N. A. (**1949**). The fauna of sand and mud banks near the mouth of the Exe estuary. *J. Mar. Biol. Ass. U.K.* **28,** 189-238.
Holme, N. A. (**1953**). The biomass of the bottom fauna in the English Channel off Plymouth. *J. Mar. Biol. Ass. U.K.* **32,** 1-49.
Holme, N. A. (**1954**). The ecology of British species of *Ensis*. *J. Mar. Biol. Ass. U.K.* **33,** 145-72.
Jones, N. S. (**1950**). Marine bottom communities. *Biol. Rev.* **25,** 283-313.
Knudsen, M. (Ed.) (**1901**). *Hydrographical Tables*. Copenhagen.
Krumbein, W. C. (**1936**). Application of logarithmic moments to size frequency distributions of sediments. *J. Sediment. Petrol.* **6,** 35-47.
Krumbein, W. C. (**1939**). Graphic presentation and statistical analysis of sedimentary data. pp. 558-91 in **Trask, P. D.** (ed.) (**1939b**).
Krumbein, W. C. & Pettijohn, F. J. (**1938**). *Manual of sedimentary Petrography*. New York and London.
Moore, H. B. (**1931**). The muds of the Clyde Sea Area. III. Chemical and physical conditions; rate and nature of sedimentation; and fauna. *J. Mar. Biol. Ass. U.K.* **17,** 325-58.
Murray, J. & Renard, A. F. (**1891**). Report on deep-sea deposits based on the specimens collected during the voyage of H.M.S. *Challenger* in the years 1872-76. *Challenger Reports,* 525 pp.
Piper, C. S. (**1947**). *Soil and Plant Analysis*. Adelaide.
Pirrie, E., Bruce, J. R. & Moore, H. B. (**1932**). A quantitative study of the fauna of the sandy beach at Port Erin. *J. Mar. Biol. Ass. U.K.* **18,** 279-96.
Rees, C. B. (**1940**). A preliminary study of the ecology of a mud-flat. *J. Mar. Biol. Ass. U.K.* **24,** 185-99.
Robinson, G. W. (**1922**). A new method for the mechanical analysis of soils and other dispersions. *J. Agric. Sci.* **12,** 306-21.
Smith, J. E. (**1932**). The shell gravel deposits, and the infauna of the Eddystone Grounds. *J. Mar. Biol. Ass. U.K.* **18,** 243-78.
Sverdrup, H. U., Johnson, M. W. & Fleming, R. H. (**1942**). *The Oceans*. New York.
Trask, P. D. (**1939a**). Organic content of recent marine sediments. pp. 428-453 in **Trask** (**ed.**) **1939b.**
Trask, P. D. (Ed.) (**1939b**). *Recent Marine Sediments: a symposium*. Tulsa.
Wilson, D. P. (**1953a**). The settlement of *Ophelia bicornis* Savigny larvae. The 1951 experiments. *J. Mar. Biol. Ass. U.K.* **31,** 413-38.
Wilson, D. P. (**1953b**). The settlement of *Ophelia bicornis* Savigny larvae. The 1952 experiments. *J. Mar. Biol. Ass. U.K.* **32,** 209-33.

STUDIES ON LOCAL POPULATIONS OF THE FRESHWATER LIMPET *ANCYLUS FLUVIATILIS* MÜLLER

By R. GELDIAY
Department of Zoology, University of Ankara

(With 5 Figures in the Text)

There are two British freshwater limpets: *Ancylus* (*Ancylastrum*) *fluviatilis* Müller and *Acroloxus* (*Ancylus*) *lacustris* (Linnaeus.). The names have undergone the same bewildering changes as those of most other freshwater gastropods; here the nomenclature of the Conchological Society's recent census is used (Conch. Soc. 1951). The distribution throughout the British Isles (Conch. Soc. 1951) and the ecology of both species (Boycott 1936) have been studied, but not much is known about the natural history or about the detailed distribution in a small area. The present study aims to supply some information on these topics. Unfortunately I did not know about Hunter's (1953) studies of the same animal until after the present work was complete. The investigation was carried out during a year's residence at the Windermere Laboratory of the Freshwater Biological Association, and this report on it describes first, the general distribution in the Lake District, including observations on how deep *Ancylus* goes in Windermere. Then there is an account of mating and egg-laying habits, and of an attempt to find out how many eggs an individual lays. Extensive observations were made on the course of growth and time of reproduction at two stations in Windermere and one in a small stony stream, or beck to use the local word. This leads on to a consideration of the fluctuation in numbers with the passing of the seasons and the total populations at different stations at comparable times. Finally, some observations on food and on commensals are recorded.

METHODS

For the observations on growth, specimens were removed each month from the three stations and measured with a micrometer and the fish-egg measuring trough described by von Bayer (1910). The population studies were carried out at fifteen stations along the edge of Windermere and twenty-two in five small streams flowing into that lake. It was clearly imperative not to alter the population and accordingly the method was to lift a stone, count the limpets on it, and then replace it carefully. Ten minutes counting at each station yielded figures with a rough comparative value. The same technique was used at stations visited irregularly. In water too deep for this method, trays of the type described by Moon (1934, 1936) were employed.

The food was investigated by diluting the stomach contents in 60 ml of water

and then transferring a portion to a known area of slide. Samples of the algae on the stones were taken for comparison by brushing everything off an area enclosed by a polythene bottle cut in half and removing it with a pipette.

DISTRIBUTION IN THE LAKE DISTRICT

Since Macan (1950) largely ignored the limpets when studying the ecology of molluscs in the Lake District, single collections were made from a variety of places (Table 1) in order to fill the gap which he left. *Ancylus fluviatilis* was found in Wastwater and Ennerdale, the two most unproductive lakes, in which the only other gastropod is likely to be *Limnaea pereger*, and therefore it would probably have been found in Crummock Water also if longer time had been spent looking for it. Its absence from Blelham is not surprising because that lake is entirely fringed by reeds and *A. fluviatilis* is found on bare rocks or stones; otherwise it probably occurs in all the lakes. It was taken in three high tarns, places where generally Macan (1950, p. 135) failed to find any gastropods, and also in two quarries in small pools so recent that accumulating debris had not covered the stones left on the bottom by the quarrying operations.

Table 1. *Records of* Ancylus fluviatilis

		Type of water body	Altitude (ft)	Number of specimens in 10 min
Wastwater	11 March	lake	200	23
Ennerdale	11 March	,,	368	310
Buttermere	11 March	,,	130	10
Crummock	11 March	,,	321	0
Loweswater	11 March	,,	399	320
Haweswater	15 May	,,		157
Brotherswater	8 April	,,	520	80
Ullswater	8 April	,,	476	265, 380, 122
Blelham	27 March	,,		0
Loughrigg Tarn	20 March	low tarn	308	0
Red Tarn	19 May	high tarn	2356	65
Blea Water	15 May	,, ,,	1588	144
Small Water	15 May	,, ,,	1484	120
Langdale Pikes	19 May	,, ,,	c. 2500	0
Outgate Q.	several occasions	quarry pool		present
near Hawes, Yorkshire	21 May	,, ,,		present

A number of becks near The Ferry House were examined and *Ancylus fluviatilis* was found in all but the small ones, many of which did probably not run all through the year. It was absent from the topmost reaches of the becks in which it was found, as shown in Fig. 4, but occurred all the rest of the way down. It has been noted in other parts of the Lake District and probably occurs in most becks, where it is the only gastropod.

Table 2 shows the populations on trays which were put down in shallow water near the edge of Windermere in October and subsequently examined but not disturbed each month. The trays were colonized rapidly and the experiment showed

that the technique could be used to find out how deep limpets occurred. Accordingly trays were laid at intervals at depths down to 5 m in February. The catches, set out in Table 3, show that limpets occurred down to this depth though in numbers that decreased as the water grew deeper, except in May, June and July, the breeding months, when none occurred at 5 m.

Table 2. *Number of limpets counted on trays parallel with the shore of Windermere*

Tray number	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total	Average
1	4	—	—	1	1	2	3	3	4	16	15	49	4·4
2	12	—	5	—	—	—	10	—	10	50	60	147	13·3
3	22	2	4	2	3	5	3	4	16	25	23	109	9·9
4	34	2	2	1	1	2	2	7	4	32	32	119	10·8
5	3	1	8	1	3	3	24	24	39	25	27	158	14·3
6	—	—	5	1	3	2	3	7	72	80	140	313	28·4
7	81	9	4	9	10	15	8	20	80	85	102	423	38·4
Total	156	14	28	15	21	29	53	65	225	313	399	1318	

In a further experiment, two trays were laid in water 12 m deep. One was devoid of snails, the other bore 25 adults and 100 egg capsules. The experiment started in April and continued for four months, during which time there was no colonization. Most of the eggs failed to hatch and the population gradually died out, catches being:

20 May	20 adults	0 young
16 June	16 adults	1 young
12 July	12 adults	5 young
August	nil	

There is probably insufficient light for algal growth at 12 m in Windermere.

Table 3. *Numbers of limpets counted on trays set in a line at right-angles to the shore of Windermere*

	Tray number					
	1	2	3	4	5	6
Distance off shore (m)	4	6	7	9	12	15
Depth (cm)	15	40	80	200	400	500
30 March (after 4 weeks)	5	9	2	18	—	14
30 April	13	12	7	9	—	12
30 May	16	9	14	14	7	—
30 June old	5	6	5	4	3	—
30 June young	179	99	13	12	16	—
30 July	102	62	17	15	12	—
30 August	124	96	25	17	5	8
30 September	106	80	21	13	7	5
Total	550	373	124	102	50	39
Monthly average (7 months)	78	53	17	14	7	5.5

Ancylus fluviatilis then is a remarkably ubiquitous snail; it is apparently restricted to a hard substratum but, if there is one, can tolerate much that other snails cannot. That it is not often found in stagnant water is likely to be due to the

rarity of bare rocks or stones on the bottom of such places rather than to any physiological requirement on its part. Berg's (1952) findings that *Ancylus fluviatilis* and *Acroloxus lacustris* have similar oxygen consumptions become less surprising in the light of the present records.

Little attention was paid to *Acroloxus lacustris*, except during the work on distribution. It was not found in any tarn, but was found extensively in Windermere and Esthwaite Water (Fig. 4). Most were on the stems of *Schoenoplectus lacustris*, some on the stems of *Typha latifolia* and a few on the stems of *Phragmites communis* or the leaves of water-lilies.

REPRODUCTION, GROWTH AND POPULATIONS

(*a*) *Mating, egg-laying and number of eggs*

The earliest copulation of *Ancylus fluviatilis* seen was on 23 February 1953 and and it continued throughout the summer; the time of reproduction is discussed in the next section. Surprisingly, chain copulation, which does not seem to have been recorded before (Bondesen 1950) appeared to be the rule in the Lake District (Fig. 1), and as many as seven were found together. Self-fertilization and reciprocal fertilization were not observed.

Fig. 1. A chain of individuals copulating. c.o = copulatory organ.

The egg capsules were generally laid beneath stones. It will be seen from Table 4 that the figures obtained for number of eggs per capsule and the sizes of eggs and capsules, are very close to those quoted by Bondesen (1950). Capsules with no eggs in them were found more frequently towards the end of the breeding season.

An attempt was made to find out how many capsules an individual produced. In an aquarium the maximum number laid was ten, and then the experiment ended because a change in the source of water became necessary and the new one

proved to contain a lethal concentration of copper. I have since learned from Dr Macan, who discussed the matter with Capt. C. Diver, that aquarium experiments are probably inadmissable, for when Capt. Diver was doing genetic work he noticed incidentally that the number of eggs that a snail laid was influenced both by the size of the container in which it was confined and by the frequency with which its water was changed.

Table 4. *Egg capsules of* Ancylus fluviatilis

	Windermere	Bondesen (1950)
Average size of capsule (mm)	3·42 × 2·7	3·3 × 2·8
Largest capsule (mm)	4·72 × 3·9	4·5 × 4·2
Size of egg (mm)	1·38 × 1·23	1·42 × 1·20
Number of eggs per capsule	0-11	Up to 10
Average eggs per capsule		
(200 capsules in nature)	3·99	
(55 capsules in aquaria)	4·27	

Frequency of eggs per capsule:

		Number of eggs									
		0	1	2	3	4	5	6	7	8	9
Number of capsules	st. 3	5	—	—	31	13	40	11	—	—	—
	st. 4	6	9	16	12	11	24	16	—	3	3

Some results obtained by counting the number of snails and the number of egg capsules on a series of stones in a stream are presented in Table 5. Such observations are of course subject to certain errors. In the first place a snail may move away from the stone where it oviposited. However, some experiments in which limpets were marked with a dab of nail-varnish and observed over a period of time showed that there is little moving about and, therefore, if water level is constant, there is no reason to suppose that a big error arises from this source. More likely to be important is the dying off of the adult limpets after they have laid eggs. In Wilfin Beck, the first mating was seen on 26 February, the first egg capsule on 22 April, and by late May, when the observations in Table 5 were made, the number of limpets had begun to decrease. Possibly the decrease in adults was compensated for by the disappearance of egg capsules which had been eaten. It is impossible to estimate the errors in observations of this kind made in the wild, but it is probable that the figures in Table 5 give too few adults per egg capsule. A limpet, therefore, probably lays between ten and twenty capsules, the number being more likely nearer the lower figure. The total number of eggs is perhaps about fifty. Hunter (1953) found that in Loch Lomond the average number of eggs laid by an individual was forty-six contained in about twelve capsules.

(*b*) *Growth and time of reproduction*

Growth was observed by measuring specimens from three stations every month. Both of those in Windermere were on a stony bottom, but station 10 was more exposed to wave action than station 3. The results are set forth in Table 6 and illustrated in Fig. 2, where station 3 and also the station in Wilfin Beck are shown in black and station 10 in white.

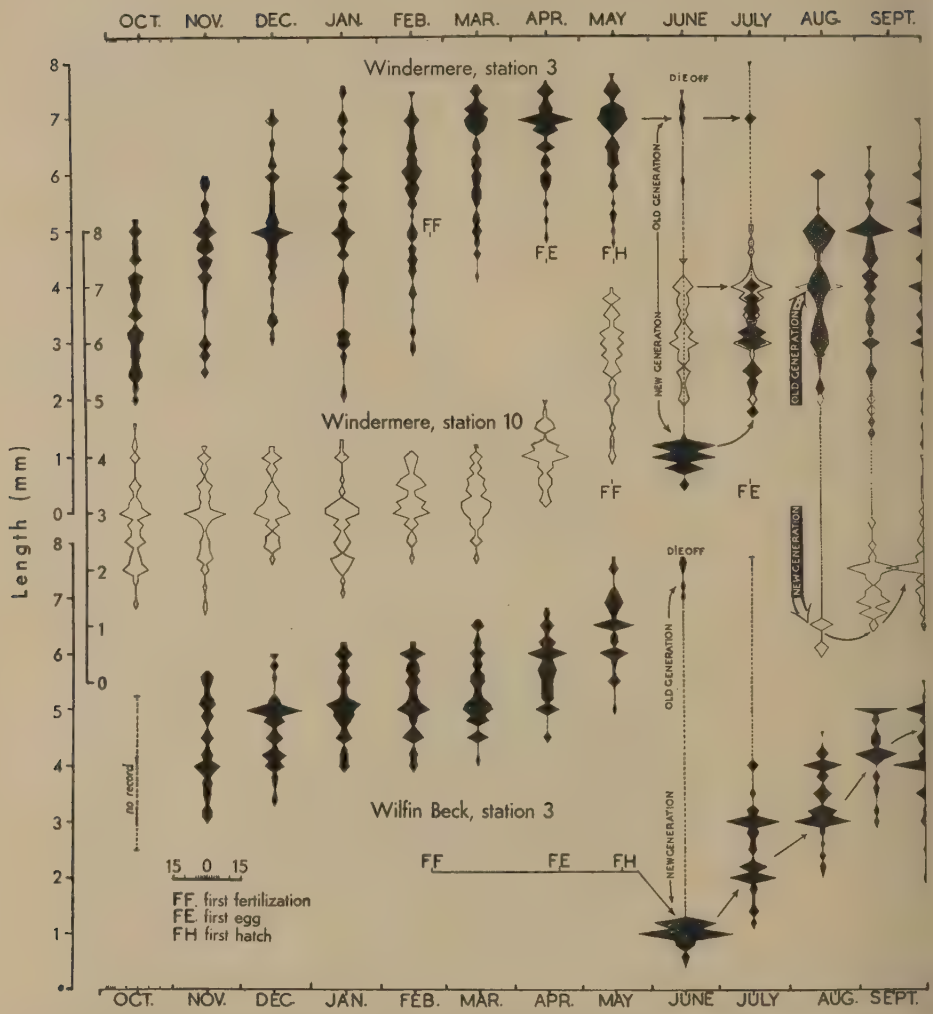


Fig. 2. Growth at three different stations. The kite histograms show the number of individuals in each size group in successive months.

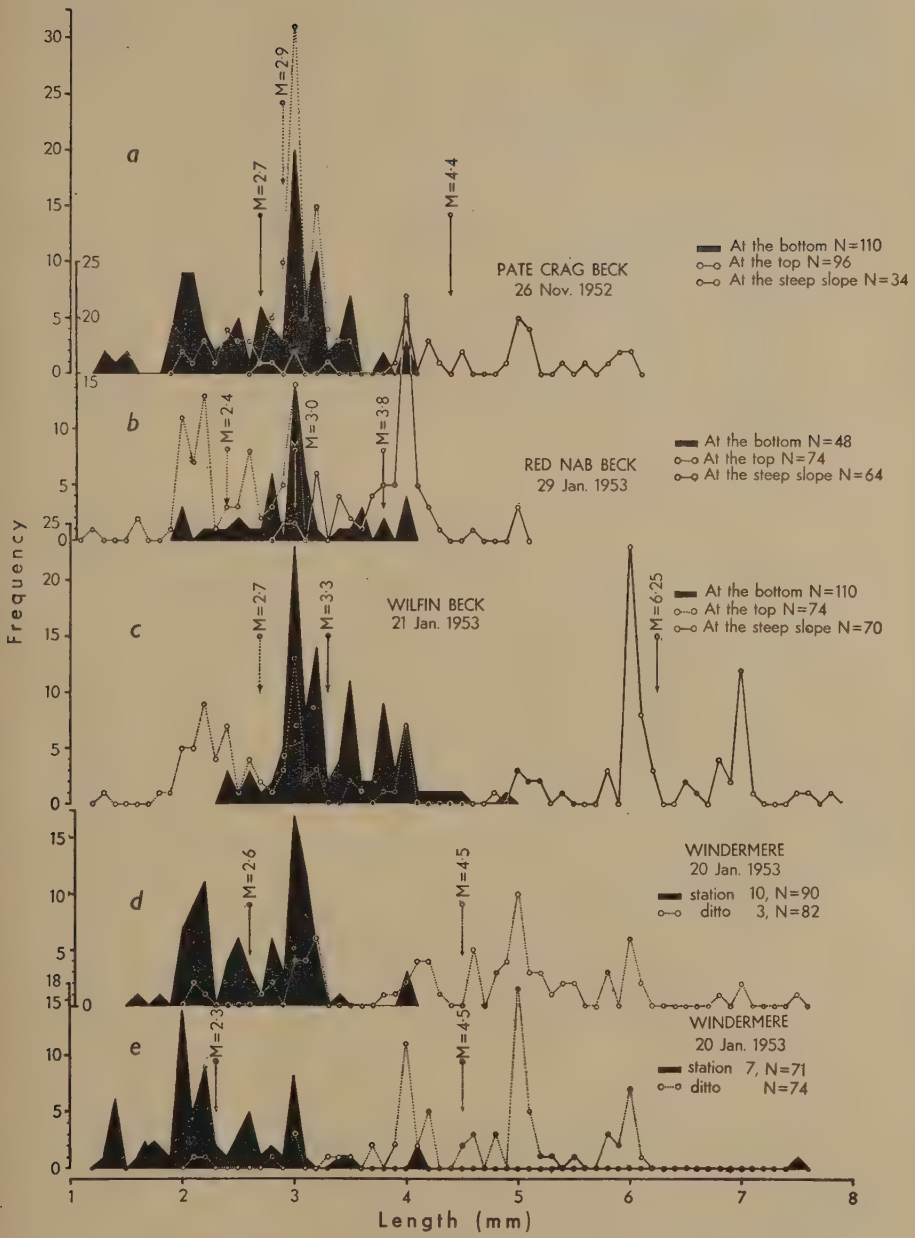


Fig. 3. Size-groups on one date at different places in three becks and one lake.

When the observations began in October, the limpets at station 3, the quiet-water station, were nearly half as big again as those at station 10, and during the winter, when both groups made slow but steady growth, they increased their lead. Early in the following year they were sexually mature, and the letters FF, FE and FH on Fig. 2 indicate respectively the dates when copulation, eggs, and young were

Table 5. *Numbers of limpets and egg capsules per stone in Wilfin Beck*

Station 2				Station 3			
Dimensions of stone (cm)	Number of snails	Number of egg capsules	Ratio	Dimensions of stone (cm)	Number of snails	Number of egg capsules	Ratio
12× 5×4	7	87	12	12×8×5	5	107	21
15× 8×6	12	220	18	8×6×4	3	54	18
8× 5×4	16	187	11	6×5×4	10	73	7
15× 8×5	8	160	20	15×5×3	9	176	19
10× 6×3	4	34	9	7×5×3	3	76	25
10×10×6	11	173	16	8×5×4	5	147	29
15× 8×4	13	234	17	15×5×4	4	170	42
12× 6×5	9	184	20	8×4×3	—	60	—
8 stones	80	1279	16	8 stones	39	863	22

seen for the first time. In May, just as the new generation is beginning to appear, the old generation is beginning to die off, in June and July there are only a few survivors and in August it has disappeared completely. In this month small specimens were found copulating, an observation which coupled with the discovery of tiny limpets in September indicates that some reproduce in the year in which they are born. As far as can be made out the offspring of these late breeders grow up alongside their parents; it will be noted in Fig. 2 and in Table 6 that the size range is greater at station 3 than at station 10. They tend to mature together in the following year and die at much the same time. This appears to be the first record of two generations in one year in *Ancylus fluviatilis*. At station 10 the sequence of events is different. The limpets are smaller than those at station 3 in the autumn, and they grow less during the winter, with the result that in the following April they are not much more than half grown, whereas the others are nearly full grown. In the early part of the summer they grow rapidly and the final size is about the same as that of the station 10 specimens, but it is not attained until about three months later and there is a similar lag in the time of reproduction. The new generation does not become abundant till September, and there is no breeding a second time. In Wilfin Beck the course of events was as at station 3 in Windermere except that there was no evidence of a second generation.

The type of growth can be judged from the size-frequency distribution at any time, and Fig. 3 shows some size-frequency distributions for winter months in Windermere and in three becks. In all the becks the station 3 type of growth, that is medium-sized specimens in winter and large ones early in the year, occurs at the stations in the steep part of the beck; the other type occurs at stations towards the top and near the bottom, specimens at the top of two of the becks being smaller than those at the bottom. In Windermere the reverse is found, the station 3 type

of growth being found where there is not so much water movement. Several hundred specimens transplanted from one place to another showed a growth-pattern typical of the new place, not of the one from which they had come.

Table 6. *Lengths of limpets at different times of year*

Each month 100 individuals were measured at each station.

	Average water temperature (°C)	Average age (months)	Length (mm) mean	Length (mm) range	Increase in 1 month
WINDERMERE STN. 3					
October	9·64	5	3·55	2·2-5·2	—
November	6·40	6	4·43	2·5-6·0	0·88
December	2·92	7	4·90	3·2-7·1	0·47
January	3·60	8	4·98	2·1-7·6	0·08
February	3·22	9	5·46	2·9-7·5	0·48
March	5·16	10	5·66	4·6-7·5	0·20
April	7·56	11	6·70	5·2-7·6	1·04
May	12·86	12	6·77	5·3-7·8	0·07
June	16·56		7·10	5·9-7·5	0·33
June (end)	16·56	1	1·00	0·5-1·2	—
July	17·96	2	3·44	1·8-4·1	2·44
August	17·70	3	4·16	2·2-6·0	0·72
September	14·68	4	4·37	1·2-7·8	0·21
WINDERMERE STN. 10					
October	9·64	3	2·75	1·4-4·6	—
November	6·40	4	2·90	1·3-4·0	0·15
December	2·92	5	2·95	2·2-4·2	0·05
January	3·60	6	2·97	1·6-4·3	0·02
February	3·22	7	3·24	2·2-4·1	0·27
March	5·16	8	3·27	2·5-4·2	0·03
April	7·56	9	4·06	3·2-4·8	0·79
May	12·86	10	5·03	3·9-6·6	0·97
June	16·56	11	5·20	4·0-7·0	0·17
July	17·96	12	6·62	5·0-8·1	1·42
August	17·70		6·88	5·0-8·1	0·26
August (end)	17·70	1	0·83	0·5-1·0	—
September	14·68	2	1·70	1·0-2·8	0·87
September (end)	14·68	2	2·06	1·0-4·0	0·36
WILFIN BECK STN. 3					
October	—	5	—	—	—
November	8·72	6	4·41	3·1-5·6	—
December	5·20	7	4·68	3·4-6·0	0·27
January	5·80	8	5·10	4·0-6·2	0·42
February	6·20	9	5·18	4·0-6·2	0·08
March	9·10	10	5·30	4·1-6·6	0·12
April	11·30	11	5·73	4·5-6·8	0·43
May	14·26	12	6·56	5·0-7·6	0·83
June	15·23		7·40	7·0-7·7	0·84
June (end)	15·23	1	1·02	0·5-1·2	—
July	13·5	2	2·51	1·2-4·0	1·49
August	13·6	3	3·36	2·1-4·6	0·85
September	10·5	4	4·18	2·0-5·5	0·82
October	10·2	5	4·41	3·1-5·7	0·23

(c) Total populations at different places and seasonal fluctuations in numbers

The fifteen stations in Windermere at which regular counts were made extend northwards from Ferry House at fairly regular intervals, and their positions are shown in Fig. 4. The lake bottom along this stretch is either what Moon (1934) calls 'Bannisdale shore' or 'drift shore'; it shelves fairly steeply and all of it is exposed to wave action.

The five becks flow off Claife Heights, a ridge of hills some 200 m high and rather steep on the Windermere side. Four of the becks flow down this steep side. Belle Grange and Nor Moss Becks have profiles with a relatively flat stretch on top of the hill, a steep stretch down the side, and another flat stretch at the bottom, clearly marked but short. At the bottom they both average about 1 m in width and are not more than ankle-deep at normal level. Red Nab Beck is smaller and Pate Crag Beck smaller still. The last of the five, Wilfin Beck, though scarcely larger than the others, is different in that it does not flow at right-angles to the ridge and therefore has a gentler gradient, though it is fast enough to be stony throughout its length. A further difference is that in its lower course it flows through agricultural land; all the stations but the highest (station 8) are in the cultivated zone.

If the total numbers of specimens collected in twelve months (Table 7) be compared one with another, it is seen that the lowest total for any station in Windermere is about 500 and the highest about 5000. There are some big differences in the number taken in successive months at some stations, probably because population density was different at places quite close together and it was not possible to sample exactly the same area each time, but on the whole each station had a population that was always poor, moderate or good relative to the others. No conclusions were drawn about the causes of the different population densities.

In the becks the range is rather greater, the lowest total in twelve months being not much over 100, the highest over 6000. Belle Grange and Nor Moss Becks had fewest specimens; Wilfin and Pate Crag Becks had most. The denser population of Wilfin Beck may have been due to its slower flow, or to a better supply of nutrients from the cultivated land through which it flowed. That of Pate Crag Beck could not have been due to the latter and was probably attributable to the small volume of water, which would have less power to roll over stones and crush the limpets than that in Nor Moss and Belle Grange, the larger becks with the sparser populations. Red Nab Beck, intermediate in size and in population, supports this theory.

The next comparison to be made is between the monthly totals. In Windermere these tend to reflect the height of the surface of the lake, because limpets do not move fast when the water rises and consequently a high level produces a low count. Conversely, a falling lake level concentrates the population and causes a big count. Some individuals are stranded when the water recedes and these are probably soon picked up by birds. In spite of this the figures suggest a rather even population throughout the year; no massive increase follows breeding and it seems probable that the mortality rate is high in the very early stages and then rather low. In the becks the population is concentrated in times of low water and diluted in times of high but the changes in width are small and the error they introduce into the monthly totals is likely to be slight. A low population in May or June is no doubt due to the fact that the collecting was done at a time when many of the old generation had died and the new one had not appeared. In none of the becks does the new generation cause a big rise in the population and the conclusion is that, as in Windermere, among those limpets that survive infancy the death rate is low.

Table 7. *Number of limpets counted in ten minutes at various stations*

	Station	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total	Average
Windermere	1	4	46	48	36	15	102	85	56	4	—	22	27	445	37
	2	18	49	58	141	95	136	140	42	31	—	68	71	849	70
	3	20	57	65	90	68	83	175	115	78	55	120	160	1086	90
	4	16	57	74	310	244	303	225	330	148	120	180	285	2292	191
	5	3	—	1	3	20	8	3	26	205	3	145	145	562	46
	6	6	38	28	25	24	24	23	46	42	8	105	120	489	40
	7	12	49	243	276	195	380	170	782	110	15	106	180	2518	209
	7a	60	62	68	52	40	183	79	310	45	18	56	90	1063	88
	7b	50	54	140	305	335	350	212	1165	555	260	280	60	3766	313
	8	3	5	13	155	90	102	105	110	55	21	50	45	754	62
	8a	65	68	420	588	565	668	510	820	528	320	205	295	5052	421
	8b	350	370	278	357	410	402	331	405	415	210	300	195	4023	335
	9	—	74	254	294	257	430	345	390	280	227	206	220	2977	248
	9a	160	188	275	248	310	473	512	570	620	180	150	175	3861	321
	10	36	273	69	294	231	390	270	397	385	680	200	80	3305	275
Total		803	1390	2034	3174	2899	4034	3185	5564	3501	2117	2193	2148	33 042	
Wilfin Beck	1		153	112	212	164	141	118	56	186	113	186	205	1646	149
	2		316	591	425	580	620	580	163	525	1050	1100	1020	6970	633
	3		431	295	321	240	438	330	235	405	475	445	450	4065	369
	4		127	95	185	171	291	190	95	410	345	406	410	2725	247
	5		57	48	71	55	65	49	7	18	125	180	160	835	75
	6		102	124	122	180	250	97	28	87	170	170	135	1465	133
	7		×	216	260	×	×	×	×	×	×	×	×	—	—
	8		×	166	127	×	×	×	×	×	×	×	×	—	—
	9		—	—	—	—	—	—	—	—		—	—	—	
Total			1186	1265	1336	1390	1805	1364	584	1631	2278	2487	2380	17 706	
Pate Crag Beck	1	80	320	203	315	301	310	295	330	303	146	560	750	3913	326
	2	69	30	95	140	95	320	225	490	420	650	850	1150	4534	377
	3	71	215	121	40	34	180	108	130	110	20	120	250	1399	116
Total		220	565	419	495	430	810	628	950	833	816	1530	2150	9846	
Belle Grange Beck	1	37	15	37	15	26	19	21	8	—	53	50	42	323	26
	2	29	42	28	52	61	77	78	71	55	226	80	66	865	72
	3	12	6	—	2	3	1	5	3	—	45	25	25	127	10
	4	43	6	—	9	3	1	35	3	14	8	5	6	133	11
	5	27	55	2	8	31	22	30	2	1	28	10	24	240	20
Total		148	124	67	86	124	120	169	87	70	360	170	163	1688	
Red Nab Beck	1		64	61	13	13	32	66	52	2	46	45	51	445	40
	2		178	81	116	154	65	122	43	2	76	80	140	1057	96
	3		26	53	18	13	9	13	1	—	2	5	7	147	13
	4		22	18	13	15	12	32	2	—	6	7	10	137	12
	5		270	255	215	330	250	160	75	22	60	56	63	1456	159
Total			560	468	375	525	368	393	173	26	190	193	271	3542	
Nor Moss Beck	1			69	40	43	64	142	120	17	80	65	70	710	71
	2			7	8	26	31	58	47	14	39	38	40	308	30
	3			20	6	6	42	47	27	7	21	28	16	220	22
Total				96	54	75	137	247	194	38	140	131	126	1238	

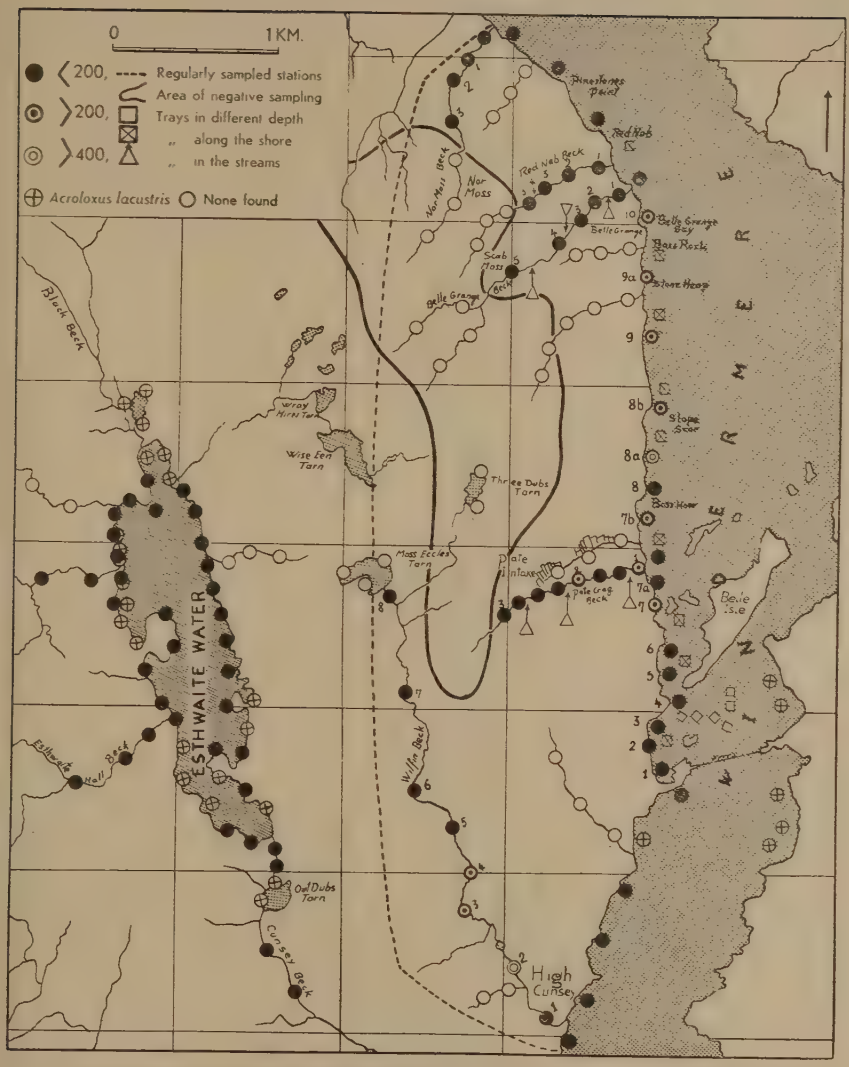


Fig. 4. The sampling stations and the distribution of the two species in part of Windermere, Esthwaite Water and neighbouring streams.

To the human a limpet appears a difficult thing to prey on though Pentelow (1932) records them in the stomachs of trout.

FOOD

A comparison of the contents of thirty stomachs with the flora of the substratum (Fig. 5) suggests that the limpets browse indiscriminately on the algal felt that covers the rocks and stones where they live. They showed no particular preference for submerged lichens as did the specimens observed by Schmid (1932). Large amounts of sand were found in the stomachs.

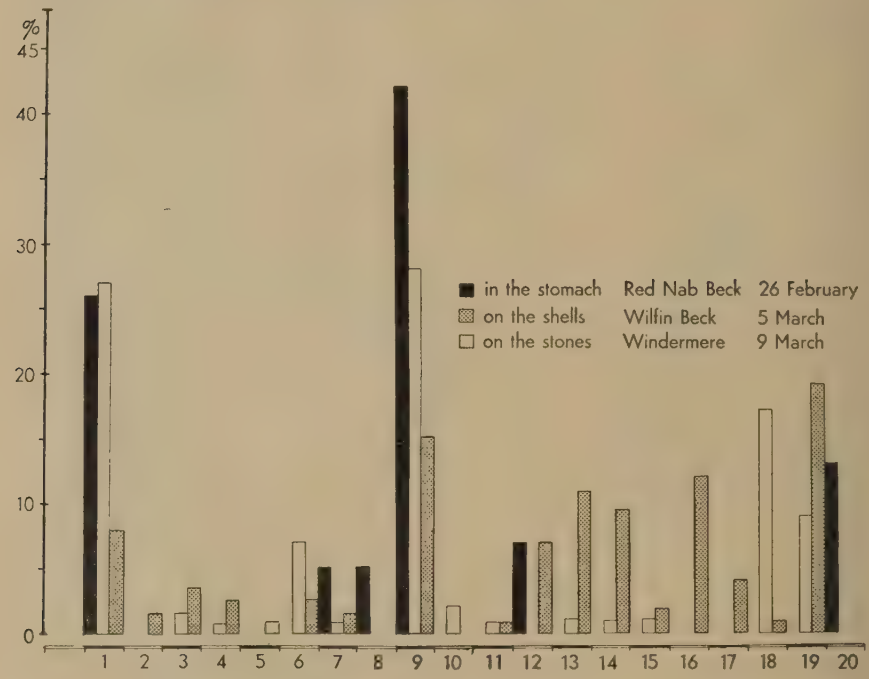

%
45
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
in the stomach Red Nab Beck 26 February
on the shells Wilfin Beck 5 March
on the stones Windermere 9 March

Fig. 5. Relative proportions of various species of algae in the stomach of and on the shells of *Ancylus fluviatilis* and on the stones where the snails were found.

1. *Achnanthes* sp.
2. *Cocconeis placentula* Ehr.
3. *Cocconeis* sp.
4. *Chantransia* sp.
5. *Cymbella* sp.
6. *Cymbella sinuata* Greg.
7. *Diatoma hiemale* Heib.
8. *Eunotia* sp.
9. *Gomphonema* sp. A.
10. *Gomphonema* sp. B.
11. *Gomphonema constrictum* Ehr.
12. *Meridian* sp.
13. *Navicula* sp. A.
14. *Navicula* sp. B.
15. *Nitzchia* sp.
16. *Phormidium* sp. A.
17. *Phormidium* sp. B.
18. *Synedra* sp. A.
19. *Synedra* sp. B.
20. *Ulothrix* sp.

COMMENSALS AND EPIBIONTS

The oligochaete *Chaetogaster limnei* Baer., which may live as a parasite on or a commensal with various Limnaeidae, was often found between the mantle and the disk of the foot of *Ancylus*. So also was a small light blue larva with a yellow

head which Prof. Dr A. Thienemann, to whom I tender my sincere thanks, identified as a member of the genus *Eukiefferiella* (Chironomidae). As many as five might infest one limpet and they were found all the year round.

The shells are covered with animals and plants. *Vorticella* is almost always present and there is invariably a growth of diatoms and other algae (Fig. 5). The limpets sometimes browse on each other's shells and this is observed particularly at mating time. Small ones, too, are frequently seen on the shells of older ones.

ACKNOWLEDGMENTS

I wish to express by cordial thanks to Mr H. C. Gilson, Director of the Freshwater Biological Association, for the excellent facilities and working conditions provided; to Dr T. T. Macan for much helpful supervision and advice; to Miss B. Douglas for her assistance with the identification of algae; to Mr G. J. Thompson and the laboratory staff who provided much help during the course of the work; and to Miss Margaret Walker to whose patience and perseverance I owe a greatly improved knowledge of the English language.

SUMMARY

1. *Ancylus fluviatilis* is found only on exposed rock or bare stone and occurs almost wherever there is a suitable substratum for it in both running and still waters. It is common in lakes including the least productive ones, where molluscs are few; it is abundant in stony streams, where no other gastropods are found; it was found in several high tarns, a type of place from which gastropods are usually absent; and it was recorded from two small pools in quarries. In Windermere it was found down to a depth of 5 m and planted specimens did not survive at 12 m.

2. Chain copulation seems to be the rule in the Lake District. One individual probably lays about fifty eggs in between ten and twenty capsules. Death follows egg-laying.

3. Specimens at a fairly sheltered station in Windermere bred early in the year, the new generation appearing in May. Some of this generation bred late in the same summer. There was fair growth in the winter. Specimens at a station exposed to wave action bred about three months later, had no second generation, and grew more slowly during the winter. In streams growth of the first type occurs in the steep part.

4. Population densities ranging from about 100 specimens counted in 10 min to about 6000 in 10 min were found, but the factors governing the density were not discovered.

5. Counts made once a month for a year at a number of places showed no great change in population density through the year. Presumably mortality is very heavy when the limpets are tiny and then light as long as they live.

6. The limpets appear to feed by grazing unselectively on the algal felt that covers the substratum.

7. An oligochaete and a chironomid larva live beneath the shell, probably as commensals rather than parasites.

REFERENCES

Berg, K. (**1952**). On the oxygen consumption of Ancylidae (Gastropoda) from an ecological point of view. *Hydrobiologia*, **4**, 225-67.

Bondesen, P. (**1950**). A comparative morphological-biological analysis of the egg capsules of fresh-water pulmonate Gastropods. *Nat. Jutland.* **3**, 1-203.

Boycott, A. E. (**1936**). The habitats of fresh-water Mollusca in Britain. *J. Anim. Ecol.* **5**, 116-86.

Conchological Society (**1951**). Census of the distribution of the British non-marine Mollusca. *J. Conch.* **23**, 171-243.

Hunter, W. R. (**1953**). On the growth of the fresh-water limpet, *Ancylus fluviatilis* Müller. *Proc. Zool. Soc. Lond.* **123**, 623-36.

Macan, T. T. (**1950**). Ecology of fresh-water Mollusca in the English Lake District. *J. Anim. Ecol.* **19**, 124-46.

Moon, H. P. (**1934**). An investigation of the littoral region of Windermere. *J. Anim. Ecol.* **3**, 8-28.

Moon, H. P. (**1936**). The shallow littoral region of a bay at the north-west end of Windermere. *Proc. Zool. Soc. Lond.* 1936, 491-515.

Pentelow, F. T. K. (**1932**). The food of the Brown Trout. *J. Anim. Ecol.* **1**, 101-7.

Schmid, G. (**1932**). Das Verhalten von *Ancylus fluviatilis* zu submersen Flechten. *Arch. Molluskenk.* **64**, 37.

von Bayer, H. (**1910**). A method of measuring fish eggs. *Bull. U.S. Bur. Fish.* **28**, 1011-14.

THE LIFE-HISTORY AND HOST-RELATIONS OF A HIPPOBOSCID FLY *ORNITHOMYIA FRINGILLINA* CURTIS*

By G. B. CORBET

Fair Isle Bird Observatory, and University of St. Andrews, Queen's College, Dundee

(With 4 Figures in the Text)

The Hippoboscid fly *Ornithomyia fringillina* Curtis is a common parasite of passerine and other land birds in most parts of the British Isles. The closely related species *O. avicularia* (L.) has a more southerly distribution being absent as an established species from most of Scotland. Published information on the life-history of these flies is very scanty and has mostly been deduced from casual collecting data. It has recently been summarized by Bequaert (1953) and by Thompson (1954). The adults are found from April to November but are most abundant during July and August. They are rarely found away from their hosts where both sexes feed entirely on blood. Larvae are laid singly and at the time of deposition they are already immobile and the integument is in the process of hardening and darkening to form the puparium. Few observations have been made on the reproduction of *Ornithomyia* but much has been postulated by analogy with the pigeon fly *Pseudolynchia maura* Bigot, investigated by Coatney (1931), and the sheep ked *Melophagus ovinus* (L.) which has an extensive literature (summarized by Bequaert 1953).

The investigation described here was carried out at the Fair Isle Bird Observatory, Shetland, in 1954, and is entirely concerned with *Ornithomyia fringillina*, since *O. avicularia* only occurs there as a rare straggler on migrant birds. Some reference will be made to preliminary work done in 1953 and use is also made of some results obtained on Fair Isle in previous years. The birds primarily concerned were five breeding passerine species, namely: starling (*Sturnus vulgaris*), wheatear (*Oenanthe oenanthe*), rock pipit (*Anthus spinoletta*), meadow pipit (*Anthus pratensis*) and twite (*Carduelis flavirostris*). Many other species, mainly migrants, were examined in smaller numbers and details of these have been published separately (Corbet 1955). Altogether data are available for 1046 birds examined during 1954, from which 772 flies were collected. The main facts of the life-history were deduced from the collecting data along with a detailed examination of each fly, whilst much important information was obtained from an experiment lasting 8 weeks involving the marking and recapturing of individual flies; 560 flies were used in this experiment.

* Bequest (Thompson 1954) considers this form and *O. lagopodis* Sharp conspecific.

HABITAT AND BREEDING BEHAVIOUR OF THE HOSTS

Fair Isle has an area of about 3 sq. miles and is 25 miles from the nearest land, being equidistant from Orkney and Shetland. The result is that from the time the flies emerge in June until mid-August there is virtually no interchange of the birds which act as their hosts with those of the neighbouring breeding populations. Beginning in mid-August, however, there is a considerable southward passage of certain birds through Fair Isle from Shetland and further north.

The northern part of the island in which most of the trapping was carried out consists of rough moorland pasture. The southern part contains richer pasture with scattered patches of arable land, and an abundance of dry-stone walls. The whole island is surrounded by cliffs.

Since the life-history of the parasite must be closely related to the behaviour of the host, some of the more important differences in behaviour between the host-species may be noticed here. All the five species of birds mentioned above were nesting in the trapping area. The wheatear is abundant all over the island, nesting in holes in the ground or under boulders and walls. The minimum population of wheatears in 1951 was estimated by Williamson (1951) from recaptures of ringed nestlings to be just over 280 pairs. As the average brood size was estimated at 4·83, this gives a total population of just under 2000 birds. The wheatear is a complete migrant, leaving the island at the end of August and not returning until April. It has only one brood per year, and the very few late broods can be attributed to failure in the first attempt. All the other species are double-brooded to some extent and except for the meadow pipit are largely resident. The rock pipit is equally numerous and also nests in holes and crevices, mainly on the cliffs. The starlings nest almost entirely in holes in the field-walls and tend to return to the same nests in successive years. The juvenile starlings form flocks as soon as they are independent and each may contain as many as a hundred birds by August.

Both meadow pipit and twite nest on the ground among long grass and heather and show no tendency to return to the same nesting site in successive years. Twites also tend to form large flocks.

Probably the only other species present which could act as regular breeding hosts for the flies are house sparrow (*Passer domesticus*), skylark (*Alauda arvensis*) and wren (*Troglodytes troglodytes*). The first nests abundantly in the southern part of the island and some juveniles trapped were infested, but too few were trapped to give any significant results. No skylarks were trapped at all but it is almost certain that they are also infested since they nest in the same habitat as the meadow pipits. The wren population is small and scattered.

These are all the small breeding passerines present on the island. Some of the other breeding birds may possibly harbour flies but their numbers are small and probably insignificant. Flies have been seen on chicks of arctic skua (*Stercorarius parasiticus*), oystercatcher (*Haematopus ostralegus*) and snipe (*Capella gallinago*), whilst a puparium was found in the nest of a ringed plover (*Charadrius hiaticula*). No flies have been recorded from the cliff-nesting sea-birds.

METHODS

Most of the birds were trapped by means of the five permanent Heligoland traps of the Observatory, which extend for about a mile to the south of the Observatory itself. In addition small automatic 'Potter' traps were used with great success, sited on the rotting seaweed on the shore. Baited with glass tubes containing living seaweed flies, they were responsible for many retrappings of rock pipits and wheatears which both feed commonly on the shore. Sometimes more than one bird was present in the catching-box of a Heligoland trap at one time and it is therefore possible that flies could at times have changed hosts in the catching-box; but this is unlikely to have been a frequent occurrence and there is no evidence of it from recoveries of marked flies. In every case when a marked fly was found to have changed hosts the possibility of exchange in the box was considered but the original host was never found to have been present in the same box. Immediately on removal from the trap each bird was placed in a clean muslin bag which was then tied at the top to prevent flies from escaping. The flies were removed from each bird immediately on removal from the bag. This was done by means of a specially designed chloroform-vapour apparatus which has been described by Williamson (1954). After treatment of the bird the empty bag was always inspected for flies and puparia. This method is considered to be 100% efficient in removing the flies. Since this is assumed throughout the analysis of the results, the evidence on which it is based is given below. After treatment, each bird was measured, ringed and carefully examined for moult. Never during this process was a fly seen in the plumage nor seen to fall or fly from a bird. During treatment the flies which were obtained all appeared within a short period of time and continued treatment and fluttering of the bird always failed to produce further flies. Many individual birds, particularly rock pipits, were trapped repeatedly, almost daily in a few cases, and were released carrying marked flies. In cases where marked flies were recovered on the same bird this was invariably on the first treatment after release.

During the period of the marking experiment the flies were removed from the apparatus immediately after treatment of the bird and placed in individual glass tubes. Each fly was examined while it was anaesthetized and details noted of sex, state of gravidity of females, damage to legs or wings, number and position of any feather lice or mites, and any peculiarity of colour or structure observed. The abdomen of the female was not measured but each was given a number according to an arbitrary scale from 1 to 6, in which size 2 was the normal condition (abdomen equal to thorax) while size 6 was fully gravid. Much interesting information was obtained on the occurrence of feather lice (Mallophaga) and mites on the flies but as they are not believed to have any important effect on the life-history of the fly, the details are being published separately (Corbet 1956).

The marking was done by means of cellulose paint while the fly was anaesthetized. Each fly received three spots of paint, two on the dorsal surface of the thorax

and one on the ventral surface of a femur. Using four colours of paint, this allows 768 different arrangements. In fact 560 flies were marked in this way.

One marked fly was released in the plumage of each bird (on the flank under the wing) as it was being set free. It was put on any of the five species irrespective of its original host. All the birds were given a numbered ring and were released at the Observatory. A total of 63 flies was released without a host in different parts of the trapping area. Marked flies were released every day during the eight weeks of the experiment.

DEGREE OF INFESTATION

Throughout this and the following sections all figures unless otherwise stated refer to 'new' birds only and disregard all birds which had already been trapped and examined during the period of the investigation.

During the period of maximum abundance of the flies a large proportion of the birds was infested. Considering the whole of July, 75% of all wheatears trapped were infested and 38% of twites, the other species being intermediate. The highest number of flies found on one bird was ten on a juvenile wheatear but one was the commonest number. Table 1 shows the frequencies of the different degrees of infestation. 21 June was chosen as the early limit since no juvenile birds were examined before that date.

Table 1. *Summary of degree of infestation (21 June to 29 August)*

Figures represent numbers of birds.

	Number of flies on each bird											
	0	1	2	3	4	5	6	7	8	9	10	Total
Starlings	47	30	17	11	3	5	2	1	1	0	0	117
Wheatears	107	48	31	16	7	2	1	2	1	0	1	216
Rock pipits	104	56	33	17	4	2	0	1	0	0	0	217
Meadow pipits	75	23	13	3	1	1	0	0	0	0	0	116
Twites	47	7	5	2	0	0	0	0	0	0	0	61
Total birds	380	164	99	49	15	10	3	4	2	0	1	727

The differences in degree of infestation between the five species is shown in Table 2 which includes juvenile birds only, from their first appearance until 29 August. The corresponding figures for the island of Skokholm, Pembrokeshire, calculated from data given by Stansfield (1955) are given for three of the species. The absolute values of these figures cannot be compared with those from Fair Isle since they refer to a longer period, but it is interesting to note that the species occur in the same order as on Fair Isle. The figures for wheatear and twite in 1953 are abnormally low due to the capture of unusually large numbers of these species in the latter part of the period when flies were becoming scarce. The significance of the differences shown in the 1954 Fair Isle column was investigated using the *t*-test. It was found that the only significant difference between adjacent species in the table was that between rock pipit and meadow pipit ($t = 3{\cdot}05$, $P < 0{\cdot}01$). However, the difference between starling and rock pipit is also significant ($t = 2{\cdot}66$, $P < 0{\cdot}01$).

Several factors are probably operative in determining the extent to which each species is infested, the most important being nest-site and body-size. Since suitable nesting-holes are limited, there is a tendency for the hole-nesting species—starling, wheatear and rock pipit but particularly the starling—to return to the same hole in successive years. In this way these species suffer added infestation from flies emerging from puparia dropped in the nest during the previous summer. On the other hand meadow pipit and twite are not exposed to this as they choose a different nesting-site each year. It also seems likely that at open nests the parent birds will kill any flies they happen to see in the nest or on the nestlings while those nesting in dark holes would not be able to do so to the same extent.

Table 2. *Differences in infestation between juveniles of each host species*

	Number of birds examined			Mean number of flies per bird examined			
				Fair Isle			Skokholm
	1952	1953	1954	1952	1953	1954 (±S.E.)	1954
Starling	67	45	116	2·35	2·58	1·40 ± 0·16	—
Wheatear	205	223	200	1·33	0·89	1·11 ± 0·11	0·80
Rock pipit	105	157	212	0·81	1·08	0·97 ± 0·10	0·56
Meadow pipit	120	92	113	0·72	0·93	0·57 ± 0·09	0·50
Twite	39	98	46	0·18	0·16	0·41 ± 0·11	—

In Table 2 the species are listed in decreasing order of size. The data for the wren, though scanty, support the view that body-size is an important factor. From nine juveniles examined in July and August 1954 and eleven up to 9 August 1955 only three flies were taken, a mean of 0·15 per bird examined. The wren is even smaller than the twite but it nests in holes and so in this case body-size appears to be the more important factor.

Adult birds are very much more trap-shy than juveniles and very few were trapped during the summer. The small numbers do not allow the species to be treated separately but the combined data for all five species show that they were significantly less heavily infested than the juveniles (Table 3). Subjecting the final figures in Table 3 to the *t*-test, $t = 2{\cdot}757$ and $P < 0{\cdot}01$. The difference in percentage of birds infested is also significant ($\chi^2 = 9{\cdot}320$, $P < 0{\cdot}01$).

Table 3. *Difference in infestation between adults and juveniles*

	Number of birds examined	Number infested	Percentage infested	Mean number of flies per bird examined (±S.E. of mean)
Juveniles	685	345	50·4	0·980 ± 0·044
Adults	42	11	26·2	0·476 ± 0·132

The adult infestation figures for starling, wheatear and rock pipit on the one hand (15 birds examined) and meadow pipit and twite on the other (17 birds examined) were found to be identical, a mean of 0·47 flies per bird examined in each case. This means that the difference shown in Table 3 is due to the former species only. This supports the view that the nest-site is important in determining the degree of infestation of juvenile birds through the removal of flies from the

nestlings by adult birds at open nests, since this factor affects the young birds only. Johnson (quoted by Thompson 1938) found that juveniles were more heavily infested than adults in several species of birds in New England. Thompson (1940) giving records for both species of flies, mostly from England, found that seven adults out of forty-three were infested (16%) and fifty-four juveniles out of sixty-nine (78%). Ash (1952) gives records for both species from Berkshire and states, referring to combined data from several host species: '37·1% of the total number of birds examined were infested and of this total 6·2% were broods of young, 71·6% were juveniles and 22·2% were adults.' These figures are rather misleading since many more juveniles were examined. From the data given in this case it can be calculated that for both adults (48 birds examined) and juveniles (143 birds examined) the percentage infested was exactly the same (40%). However, the actual number of flies per bird may well have been greater on the juveniles but this information is not given. The explanation of these differences will be discussed later in the light of additional information.

SEASONAL DISTRIBUTION

The first fly obtained in 1954 was from an adult wheatear on 2 June, and the next was on a garden warbler (*Sylvia borin*) (a migrant) on 19 June. The first juvenile birds (starling, rock pipit and meadow pipit) were trapped on 25 June and most of them were infested. Flies were abundant on all species during July and August. Only 30 flies were obtained in September, mostly during the first week, and of these 17 came from migrant merlins (*Falco columbarius*). The last fly was on a redwing (*Turdus musicus*) on 26 October. The only other October fly was on a yellow-headed wagtail (*Motacilla citreola*) on the 1st.

For the purpose of analysing the changes in the degree of infestation throughout the season, the season was divided into five-day periods for each of which the percentage of birds infested and the mean number of flies per bird examined were calculated for each host species. The latter values are most useful for illustrating the seasonal fluctuations and were used in Fig. 1. The values used in the graphs are ten-day moving means taken at five-day intervals. For instance the first value is based on the period 21-30 June, and the second on the period 26 June to 5 July. The graphs for wheatear and rock pipit are most easily explained and are the most reliable, being based on the largest numbers of birds. The double peak in the rock pipit graph is obviously related to the fact that that species is double-brooded. The wheatear, which is single-brooded, only shows one peak. The graph for starling is based on fewer birds but also shows two main peaks. If differs from the rock pipit one in that the second peak is the larger. This was the only species in which first- and second-brood juveniles could be easily distinguished since the juvenile plumage is retained for a considerable time before moulting begins. In the rock pipit on the other hand moulting sometimes starts only a few days after fledging is complete. Therefore with the starling it was possible to plot the graphs for first and second broods separately. It can be seen that the second peak in the main graph is largely due to a very high degree of infestation of the second-brood

young but also that there is a simultaneous increase in infestation of the first brood. This is probably due to the flocking habits of the young starlings. Second-brood birds often join flocks of first-brood birds which could then become infested through flies changing hosts within the flock.

The horizontal section of the wheatear graph can similarly be interpreted as a reflection of the second peak of the starling and rock pipit graphs which occur at the same time. The results of marking (see next section) show that exchange of flies between different species is much less than that within species and therefore only a slight effect would be expected in the wheatear graph. The slight peak in

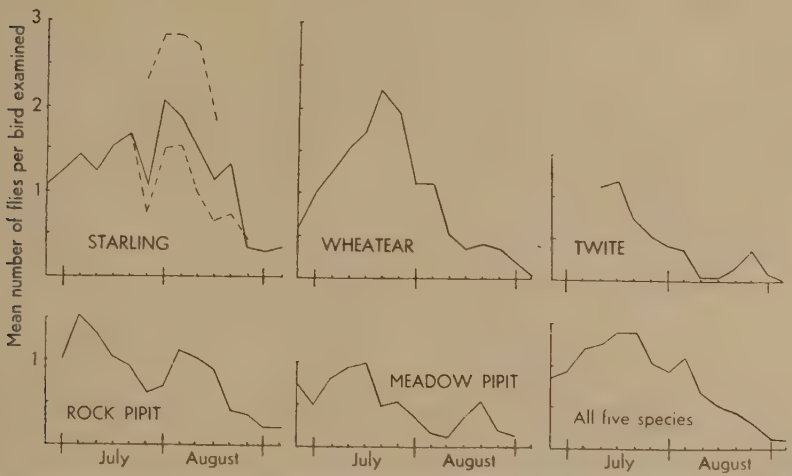


Fig. 1. Seasonal distribution of flies. Values are ten-day moving means at five-day intervals. Broken lines—1st brood (below) and 2nd brood (above) plotted separately.

the second half of August in the wheatear graph is probably due to the influx of wheatears from Shetland which occurs at this time. Butterfield (1952), in analysing the infestation of wheatears on Fair Isle in 1951, found a very great increase in the percentage of birds infested at this period, 81·7% of the wheatears being infested during the period 16-23 August compared with 25% for the previous five days. This increase coincided with a very large passage of wheatears that year which Williamson & Butterfield (1952) considered had come from the Faeroes via Shetland. A similar passage took place in 1954 but was much smaller, and the corresponding figures for fly infestation are 24% rising to 33%. It thus appears that the population of flies in the Faeroes is much higher at this time than at Fair Isle, and this may be a reflection of a later period of emergence in the Faeroes, synchronized with a later wheatear breeding season.

The graphs for meadow pipit and twite are based on too few birds to draw any very definite conclusions. In the case of the meadow pipit at least, the late August peak is probably due to immigration from the north as in the case of the wheatear. The final peak in the graph for starling could be interpreted as a reflec-

tion of these corresponding wheatear and meadow pipit peaks due to exchange of flies from these latter species to starlings.

The data immediately available for 1952 and 1953 are not strictly comparable with the 1954 figures since retrapped birds which had already been examined were included. Nevertheless they produce graphs which are very similar to those for 1954, with two exceptions. That for starling in 1952 shows only a single peak, suggesting few or no second broods that year. This conclusion is supported by the bird-ringing records for 1952. The graphs for meadow pipits for both previous years show 'second-brood peaks' in early August as well as the end of August peak.

CHANGE OF HOST

The only previous attempt to study the movement of *Ornithomyia* by marking appears to be that of Ash (1952). He marked and liberated twenty-nine *O. avicularia* and thirty-eight *O. fringillina*, only two of these being replaced on birds. One recovery was obtained. A fly from a juvenile robin (*Erithacus rubecula*) was released on an adult chaffinch (*Fringilla coelebs*) and recovered two days later on another robin.

Table 4. *Recapture data for marked flies*

	Number released	Number recaptured (and % of released flies)			Number recaptured on different birds				
		Total	On same bird	On different bird	Meadow pipit	Rock pipit	Wheat-ear	Starling	Twite
Meadow pipit	86	18(21)	12(14)	6(7)	3	0	2	0	1
Rock pipit	262	59(22·5)	46(17·6)	13(5)	0	11	2	0	0
Wheatear	143	11(7·7)	9(6·3)	2(1·4)	0	1	1	0	0
Starling	68	1(1·5)	0	1(1·5)	0	0	0	1	0
Twite	23	3(13)	2(8·7)	1(4·3)	0	0	0	0	1
All species	582	92(15·7)	69(11·7)	23(4·0)					
Set free (no host)	63	8(12·7)			1	4	3	0	0
Total	645	100(15·4)							

The mean interval before recapture was 5.5 days.

The success of the present experiment is shown in Table 4. In this table flies which were recovered and released again are considered as different flies and are counted twice. It will be seen that the great majority of recoveries were from the same individual birds on which the flies had been released. One female fly was recovered after forty-two days on the bird on which it had been released. There were twenty-three flies, however, which were recovered on a different host (25% of the total number recovered). Of these seventeen (18·5%) were on different birds of the same species while only six (6·5%) had changed host species. In all these cases of change of host there was no tendency to return to the host species from which the fly had originally been collected. Only seven out of the twenty-three did so. A similar result arises from the eight recoveries of flies released without a host. Details of these are given in Table 5 which also contains three such recoveries in 1953. The species on which they were recovered bear no relation to their

original host species. It therefore appears that a fly without a host will attach itself to the first bird it comes across irrespective of species. The crossing over from one bird to another probably occurs when birds are in close proximity, e.g. while feeding or roosting together, and will therefore, as recorded above, more often take place between members of the same species. To quote one particular case, a marked fly was released on an adult rock pipit which was colour-ringed and was observed at this time to be feeding fledglings on the shore. This adult was recovered four days later when it was found to be free of flies and it was given another marked fly. Three days later both these flies were recovered from a fledgling rock pipit which was trapped on the shore, presumably the offspring of the adult bird concerned. A case of flies seen flying freely between pipits on Skokholm Island was recorded by Thompson (1938).

Table 5. *Recoveries of flies released without a host*

	Original host	Recovered on	Time interval
1953	Wheatear	Wheatear	3 days
	Wheatear	Wheatear	1 day
	Wheatear	Wheatear	1 day
1954	Starling	Wheatear	1 day
	Wheatear	Rock pipit	4 days
	Wheatear	Rock pipit	4 days
	Rock pipit	Rock pipit	9 hours
	Rock pipit	Wheatear	6 days
	Rock pipit	Wheatear	4 days
	Rock pipit	Meadow pipit	1 day
	Meadow pipit	Rock pipit	6 days

The question of juvenile and adult infestation may now be reconsidered. It seems likely that a newly-emerged fly in the spring will attach itself to the first bird it comes across. If this bird happens to be an adult as is most likely early in the season, the fly will eventually be carried to the nest where sooner or later it will have the opportunity to transfer itself to one of the nestlings. It must be presumed that the young birds are more attractive to the fly than the adults. This could be due to a difference in texture of the skin for example. In this way flies will accumulate on the nestlings until they fledge. With the second brood this accumulation would be taking place at a period of greater abundance of flies, hence the very high infestation of the second-brood starlings shown in Fig. 1.

A particular case of exchange of flies is seen in birds of prey which feed on small birds. A merlin (*Falco columbarius*) trapped on 22 August had two flies, one of which was marked. Although through loss of paint its exact identity could not be decided, it had certainly been released on one of the local passerines about a week previously. Another merlin produced a fly which had six feather lice (*Sturnidoecus sturni* Schrank) and twenty mites (*Microlichus avus* Trouessart) attached to it. These were both characteristic of flies from starlings. Every merlin trapped during the autumn migration, a time when flies were scarce on island birds and migrants alike, was heavily infested with an average of 3·4 flies per bird. From a juvenile Montagu's harrier (*Circus pygargus*) in Co. Durham on 19 July Ash (1952) counted no less than fifty *Ornithomyia fringillina*. As both these species feed largely on

birds, it seems inevitable that they should accumulate the flies from their prey. On the other hand Bequaert (1953, p. 225) attributes the heavy infestation on birds of prey to large body-size and ill-adaptation of the bill to preening. Although the former may apply, I do not agree that birds of prey are inefficient at preening. From observations made on captive birds it appears that by using the tongue against the tip of the upper mandible quite delicate preening operations can be performed.

LONGEVITY

For reasons discussed later it seems likely that few or no flies emerge after about the middle of July, there being but one generation per year. The longest period for which a marked fly was known to survive was fifty days. This was a female fly obtained on 17 August from a wheatear and after several retrappings finally recovered on 6 October from a rock pipit on which it had been released on 25 August.

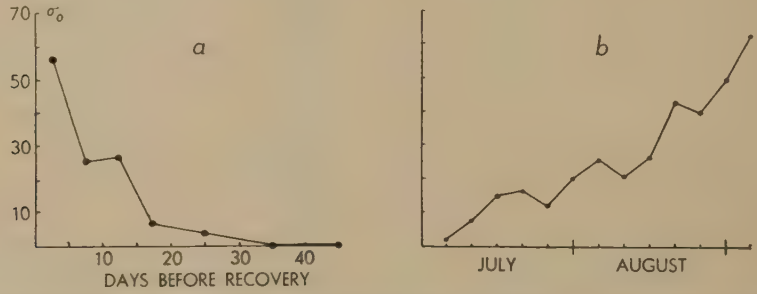


Fig. 2. Loss of marked flies and incidence of damaged flies: *a*, percentage of birds recovered with the same fly; *b*, percentage of flies damaged.

The decrease in numbers of flies after their period of greatest abundance appears to be quite uniform as can be seen from the wheatear graph in Fig. 1, neglecting the latter half of August. The gradual loss of flies (but not always necessarily their death) can also be seen from the recoveries of birds released with marked flies, as is shown in Fig. 2*a*. This graph refers to all five species of birds. Of birds recovered within five days of release 56% still carried the marked flies released on them, while of those recovered from five to ten days later only 25% still had retained their flies. The only apparent agent involved in reducing the number of flies is the preening activity of their hosts. It is interesting in this connection to examine the number of flies which were found to have damaged wings or legs. The percentage of damaged flies rose from 2% to 62·5% during the season (Fig. 2*b*). The only conceivable ways in which a fly could sustain a torn wing (and some wings were torn to shreds) or a missing tarsus, are by being snapped at by the bird's bill or, in the case of a female fly, by the claws of the male during mating. However, of 229 male and 299 female flies examined before 15 August (males become scarcer after then) thirty-six and forty-seven respectively were damaged, exactly 15·7% in each case. It can therefore be assumed that the damage is caused entirely

by the host. The extent to which marked flies are lost differs between the five host species as shown in Table 6. It will be seen that when the percentages are placed in decreasing order, the order of the species is the same as in Table 2, with a similar large difference between rock pipit and meadow pipit, i.e. the greater the degree of infestation, the greater the rate of loss of flies. This could be due to the greater exchange of flies in the case of the more heavily infested species or to a greater death-rate of flies through preening. However, a similar difference can be seen in comparing the gradients of the graphs in Fig. 1. The gradient during the main decline after the peak is greatest for starling and least for the meadow pipit. Therefore this difference must in part at least be due to a difference in death-rate.

Table 6. *The loss of marked flies by each host species*

	Starling	Wheatear	Rock pipit	Meadow pipit	Twite
Number of birds recovered	3	31	143	23	4
Number of above which lost marked fly	3	22	97	11	2
Percentage which lost fly	100	71	68	48	50

Both sexes can live for several days without food. Twenty-one flies which emerged during May and June 1955 from puparia collected on Fair Isle in 1954 were kept individually in large glass tubes until they died. They lived for 2 to 7½ days, the average being 4½ days. There was no significant difference between the sexes (ten were males). This indicates the amount of time available to a fly on emergence to locate a host.

REPRODUCTION

(*a*) *Sex ratio*

A summary of recorded sex ratios for many species of Hippoboscids has been given by Bequaert (1953, p. 176). All results based on the rearing of puparia give approximately a 1 : 1 ratio but in most collections of adult flies females predominate. No previous results based on emergences from puparia have been recorded for *Ornithomyia*. Of twenty-four flies which emerged from puparia collected on Fair Isle in 1954 thirteen were male and eleven female. In collections of flies females usually predominate slightly, but one lot of *O. fringillina* collected by Ash in Berkshire contained 60·4% males. Thompson (1955) giving records of *Ornithomyia* spp. from British bird observatories in 1952 recorded 72% females and commented on the continual preponderance of females, but this was obviously due to the fact that most of the records were from the autumn. If the proportion of females in June and July is worked out separately it is found to be 58% and that for August and September 80%. In a collection made throughout the season Ash (1955) found sixteen males and seventeen females of *O. avicularia* and seven males and six females of *O. fringillina*.

The total sex ratio for Fair Isle was 40·5% males. Fig. 3 shows the seasonal fluctuations. It will be seen that the initial ratio is approximately 1 : 1 but that the males die off more quickly than the females during August. This shorter life

of the male is also illustrated in the recovery data for marked flies. The recovery rates for the separate sexes are shown in Table 7. Firstly the total recovery rate

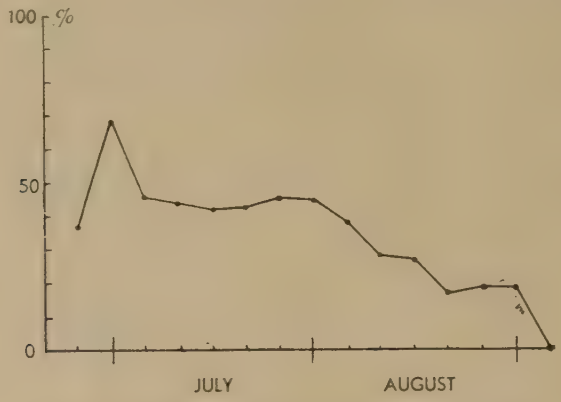


Fig. 3. Seasonal fluctuation of the percentage of male flies.

is much smaller for the male, 9·1% as compared with 19·8%, suggesting a higher death-rate. When the figures for July and August are considered separately it can be seen that in the male the recovery rate is only half as great in August as in July, whereas in the female it is the same. This is in accordance with the decrease in the proportion of males in the population during August, and suggests that in August there is, besides predation by the host, an additional factor producing death in the males which is not operating with the females, e.g. a shorter natural life-span.

Table 7. *Comparison of the recovery rates of the sexes*

	Males	Females
Number of flies released on birds	209	369
Total number of flies recovered	19 (9·1%)	73 (19·8%)
Number released in July	152	200
Number of above recovered	16 (10·5%)	39 (19·5%
Number released in August	57	169
Number of above recovered	3 (5·4%)	34 (20·1%)
Number recovered on different birds	10	13
Percentage of total recoveries on different birds	52·5%	17·8%

Table 7 also shows a considerable difference in activity between the sexes; 52·5% of males recovered had changed host but only 17·8% of females. Since all marked flies were released singly on birds which were otherwise free of flies, it is possible that a male fly finding itself alone on a bird may tend to leave it and seek another host. But it is more likely that it is merely more active than the female since in cases of natural infestation by a single fly males are almost as frequent as females; 17·8% of all males occurred singly and 20·6% of females. This greater activity of the males may be responsible for the greater death-rate, even in July, due to the greater irritation of the host.

(*b*) *Site of larviposition*

In all Hippoboscidae the females deposit single, fully-grown larvae which are immobile and pupate immediately. Many authors believed that in *Ornithomyia* most of the puparia were deposited in the nest where they overwintered and reinfested the birds using the same nest the following season. However, Crichton & Campbell (1949) suggested that this was not the case and pointed out that even if it were so it would have little effect in reinfesting future broods since most nests are not used again. Thompson (1954) also believes that most puparia are scattered at random but at the same time states the belief that the presence of puparia in the nest is the explanation of the higher infestation of juveniles than of adults.

The results of examining nests for puparia are shown in Table 8. All the passerine nests were known to have contained young which fledged successfully and

Table 8. *Details of nests examined for puparia*

	Nest-site	Number of nests	Number of puparia
Starling (*Sturnus vulgaris*)	in wall	1	0
Wheatear (*Oenanthe oenanthe*)	holes in ground	9	3, 2, 2, 1, 1
Rock pipit (*Anthus spinoletta*)	under boulders	2	0
Meadow pipit (*Anthus pratensis*)	open	3	0
Ringed plover (*Charadrius hiaticula*)	,,	3	1
Oystercatcher (*Haematopus ostralegus*)	,,	6	0
Snipe (*Capella gallinago*)	,,	1	0
Arctic skua (*Stercorarius parasiticus*)		8	0
Great skua (*Catharacta skua*)	,,	3	0

all were examined within six weeks of being used. Ash (1952) also found very few puparia in nests even when there had been considerable numbers of flies present on the nestlings. In such cases it is inevitable that puparia have dropped into the nest and therefore it must be concluded that they are being removed. Further experiment is necessary to determine whether the birds themselves, or some other predators, e.g. rodents, are responsible.

There is no doubt that larviposition takes place on the bird's body. Many marked flies in all states of gravidity were released on birds and recovered on the same bird, having laid a puparium in the meanwhile. As the puparia are very smooth and shiny they cannot remain on the bird but must fall off as soon as they are laid. Since the great majority of flies are on juvenile birds it is evident that the majority of puparia will be scattered about the ground at random although there will be a concentration at communal roosting and feeding places, while the habit which juvenile wheatears have of sheltering (and probably roosting) in burrows other than the nesting-burrow for up to a week after fledging (Williamson 1951) will increase the number of puparia laid at potential nest-sites.

A few puparia were obtained directly from birds in the chloroform apparatus but in all cases they were accompanied by a female fly which from the state of its abdomen had obviously just laid a puparium. Many puparia were laid by captive flies in the laboratory but it was found that after chloroform treatment a gravid fly tended to deposit its larva no matter what stage it had reached. Small premature larvae were always inviable.

(*c*) *Duration of pupal stage*

It was formerly assumed by analogy with other species of Hippoboscidae that puparia laid early in the summer produced imagines in the same season, but Ash (1953) gave evidence, based, however, on very few puparia, that there is but one generation per year in *Ornithomyia* (this was based mainly on *O. avicularia*). The imagos emerged between 28 March and 8 June but no mention was made of the conditions under which the puparia were kept.

Throughout the summer of 1954, sixty-two puparia, apparently fully developed were collected on Fair Isle and none of these produced imagines in the same season. A note was made for each one as to whether it had been laid before or after the parent had been anaesthetized. The puparia were kept in glass tubes stoppered with cotton wool and contained in a dark box in an unheated shed. The tubes were examined twice daily in the morning and evening and a note of the temperature taken. Since the shed was made of corrugated iron, the temperatures were unnaturally high on sunny days and therefore it is likely that the emergences were earlier than under natural conditions. All the emergences took place between 0800 and 1700 h, and most occurred on the warmest days. The pupal period varied from 207 to 324 days (mean 303 days) and the order in which they emerged bore no relation to the order in which they had been laid. There was no significant difference in mean period between the sexes (male 306 days, female 300 days). Those puparia which were laid some time after chloroform treatment of the parent were less viable than those laid before or immediately after treatment, as is shown in Table 9. The actual birth of those in the left-hand column was not affected by

Table 9. *The effect of chloroform on the viability of puparia*

	Before chloroform	After chloroform	Not known	Total
Number laid	30	27	5	62
Number emerged	15	7	2	24
Percentage emerged	50	26	40	39

the chloroform but many of them were in contact with chloroform vapour after being laid. This may explain their low viability, although the imagines were always able to survive equal and even greater exposure to chloroform. There was no significant difference in size (measured as the product of length and breadth) between viable and inviable puparia (viable 6·9, inviable 7·0), indicating that the cause of inviability was not premature laying.

(*d*) *Rate of reproduction*

The actual rate of producing puparia is difficult to determine but some idea of the potential rate can be obtained from the recoveries of marked flies. Only one case occurred in which the times of two consecutive births were obtained. This was a fly which produced two fully-formed puparia at an interval of 4 days 4 hours, 30 hours of which time was spent away from a bird. Other recoveries of female flies within four days of release are listed in Table 10 to show the changes in

abdomen size. All these cases refer to flies recovered on the birds on which they had been released. The two cases of growth from 2 to 6 in two days (actually 40 and 41 hours) suggest the possibility of an even shorter interval than four days but most of the records point to a period of about four days being normal. If the average life of a fly is about four weeks, which seems a conservative estimate, this would give an average of about seven puparia per fly, which would allow the population to persist even with a pupal mortality of 70%.

Table 10. *Change in abdomen size in female flies*

Size is recorded on a subjective scale from 1 to 6; 2, abdomen equal to thorax; 6, fully gravid; P, mature puparium laid.

Time interval	Size of abdomen: On release	Size of abdomen: On recapture	Time interval	Size of abdomen: On release	Size of abdomen: On recapture
1¾ h	2	3	2 days	2	2 (2 cases)
12 ,,	2	3	3 ,,	4	P
1 day	3	4	3 ,,	3	P
1 ,,	5	3	3 ,,	4	2
1 ,,	2	2 (20 cases)	3 ,,	2	2 (2 cases)
2 days	P-2	3	4 ,,	2	3 (2 cases)
2 ,,	2	4 (3 cases)	4 ,,	5	2
2 ,,	6	4	4 ,,	1	2
2 ,,	2	5	4 ,,	2	5
2 ,,	2	6	4 ,,	3	2
2 ,,	2	6-P			

(e) *Mating*

Mating must obviously occur on the birds. O'Mahony (1950) recorded two cases of flies taken in copulation on birds on Fair Isle. Two such cases were obtained in 1954. Of a pair in copulation taken from a juvenile starling on 18 July the female was partly gravid (size 4). Another pair was taken from a meadow pipit on 17 August. When they fell into the chloroform apparatus the female was in the process of laying a puparium while the male was grasping the female although the abdomen was not in a position of copulation. They separated as they were recovering from the effects of the chloroform, but reunited after the puparium had been laid and remained in copulation for about 30 min. Similar cases of flies mating immediately after larviposition were recorded by Coatney (1931) for the pigeon fly (*Pseudolynchia maura* Bigot). In this species the flies leave the bird for larviposition but the pair unite before they leave the host.

Gravid females (abdomen 4-6) were equally abundant throughout the season (Fig. 4) showing no decline during August corresponding with the decline in males. This suggests that mating is not necessary before each larviposition. This conclusion is also supported by several other facts. A marked female which was recovered alone on a bird 42 days after release (on 6 October) was in the process of laying. It is most unlikely that a male was present during this time. Many other similar cases occurred, with shorter intervals. It was also found that females which were on birds in company with males showed the same percentage gravidity

as those on birds where males were absent. The figures, based on 205 and 175 female flies respectively, were 42·0% and 41·4% gravid.

Despite the fact that frequent mating is not necessary it appears that it does take place. Bequaert (1953, p. 180) states that in the sheep ked (*Melophagus ovinus*) repeated mating of the same female occurs when males are present. Since very few eggs are produced in the lifetime of a fly, very little sperm will be required. Nevertheless in one female dissected immediately after mating the whole uterus was full of sperm—sufficient to fill the spermathecae fifty times over.

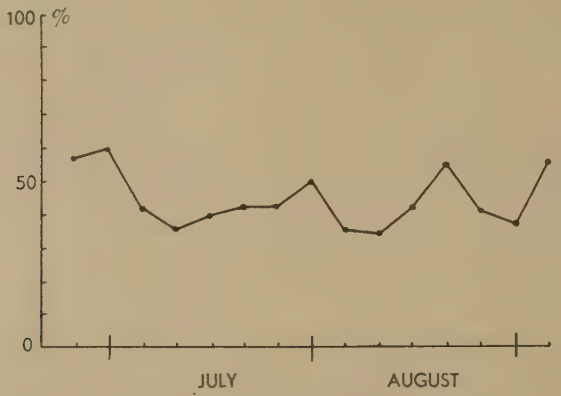


Fig. 4. Seasonal variations in the percentage of female flies gravid.

It seems quite possible that, as first suggested by Berlese (quoted by Bequaert 1953, p. 92), the sperm and the abundant secretion of the male accessory glands may play a significant part in the nourishment of the larva. It seems inevitable that the larva will imbibe this secretion since as mentioned above it may fill the uterus, and the larva, by means of a specialized cephalic pump, will take up any liquid material in the uterus. This is normally the secretion of the female accessory glands. This food supply from the male is obviously not essential for the development of the larva, but it may serve to increase the rate of larval growth. It remains to be shown whether it is absolutely incidental or whether the large size of the male organs and frequent matings are adaptations developed in connection with this function. The fact that the males are as long-lived as they are supports the view that this may be the case.

DISCUSSION

Since the life-history of the fly must necessarily correspond rather closely with that of its hosts, it is to be expected that the details will vary in different parts of the fly's range, according to the host-species present and also to the climatic conditions. The information most required to confirm and complete the present account of the situation on Fair Isle is quantitative information on the infestation of nestlings, and information on the changes in infestation of the adults throughout the nesting season.

Ornithomyia fringillina unlike *O. avicularia* is absent from the winter quarters in Africa of our migrant birds (Thompson 1954) and therefore the carriage of flies on autumn migrants can have little effect on the life-history of the fly although it will allow a slight transfer between local populations of flies.

Apart from the possible inviability of puparia many puparia must be dropped on unsuitable terrain, e.g. on the shore. In this connection it would be interesting to study more closely the distribution of *Ornithomyia* spp. with respect to habitat. In late June 1954 and in June and July 1955 six starlings and thirty-two house sparrows were trapped in a suburban district of Dundee and examined by the chloroform apparatus. All were uninfested. In addition 110 passerine birds have been trapped and eighteen broods of young examined in the same area during the last four years, in June, July and August, without a single fly having been seen, while in an area of arable land near Dundee during February 1955 forty old passerine nests were examined in vain for puparia. On the other hand on Buddon Moor, a coastal moorland near Dundee, flies have been seen on nestling meadow pipits, and puparia of *Ornithomyia fringillina* have been collected from the nest of a carrion crow *Corvus corone*. Although very incomplete, these observations suggest that *Ornithomyia fringillina* may be absent from suburban and possibly from cultivated areas, perhaps due to the lack of undisturbed ground on which the puparia can overwinter in safety. Under such circumstances, in which pupal mortality is considerable, there must be an optimum density of birds above which the chances of two flies of opposite sex arriving on the same bird would be reduced. This would lead in turn to a reduction in the number of puparia produced and the population could not persist. The concentration of birds in a suburban area may well exceed this optimum density.

ACKNOWLEDGMENTS

I am very much indebted to Mr Kenneth Williamson, Director of Fair Isle Bird Observatory, for giving me the opportunity to carry out the work, and also for making available to me the results of his routine collection of parasites from trapped birds before and after my visits and during previous years. He also gave much helpful criticism of the manuscript. Dr F. L. Waterhouse and Dr J. H. Sudd also kindly read the manuscript.

SUMMARY

1. The life-history of the Hippoboscid fly *Ornithomyia fringillina* Curtis was studied on Fair Isle, Shetland, during the summer of 1954.

2. During July and August five species of breeding passerine birds were trapped intensively and all flies were removed from each bird. Each fly was individually marked and released on another bird. A few marked flies were set free without a host.

3. The degree of infestation differed between the host species. Large body-size and the habit of nesting in holes were both responsible for heavy infestation.

4. Few adult birds were trapped, but they were less heavily infested than the juveniles in the hole-nesting species, although not in those building open nests.

5. Flies first appeared with the first juvenile birds in June, rose to a peak of

abundance in July, and were quite rare again by September. Newly-fledged birds of the second brood were very heavily infested and caused a second peak period in early August.

6. The population declined rapidly after the period of greatest abundance. Males died off more rapidly than females. The main cause of death was the preening activity of the birds. The potential length of life is probably about three or four months, the average about four weeks.

7. Of all marked flies recovered 75% were on the same individual birds on which they had been released; 18·5% had changed to other birds of the same species; 6·5% had changed to a different host species. Males changed hosts more often than females.

8. The sex ratio on emergence is probably 1 : 1 but males are slightly shorter lived than females. There is only one generation per year. Mating and the deposition of puparia both take place on the birds throughout the summer. Puparia can be laid at intervals of four days or less and fall to the ground as soon as they are laid. As the puparia must be on the ground all winter, the nature of the habitat (e.g. cultivated or uncultivated) may be important in determining the local distribution of the fly.

REFERENCES

Ash, J. (1952). Records of Hippoboscidae from Berkshire and Co. Durham in 1950, with notes on their bionomics. *Ent. Mon. Mag.* **88,** 25-30.

Ash, J. (1953). Notes on the puparial stage of some Hippoboscidae. *Ent. Mon. Mag.* **89,** 206.

Ash, J. (1955). Some records of bird and mammal ectoparasites. *Ent. Mon. Mag.* **91,** 64.

Bequaert, J. (1953). The Hippoboscidae or louse-flies (Diptera) of mammals and birds. Part 1. Structure, physiology and natural history. *Ent. Amer.* (n.s.) **32** and **33,** 1-442.

Butterfield, A. (1952). A quantitative analysis of the results of the ectoparasite study. *Bull. Fair Isle Bird Obs.* **1** (6), 38-41.

Coatney, G. R. (1931). On the biology of the pigeon fly, *Pseudolynchia maura* Bigot. *Parasitology,* **23,** 525-32.

Corbet, G. B. (1955). Records of flat-flies from migrants at Fair Isle in 1954. *Bull. Fair Isle Bird Obs.* **2** (7), 321-2.

Corbet, G. B. (1956). The phoresy of Mallophaga on a population of *Ornithomyia fringillina* Curtis (Dipt., Hippoboscidae). *Ent. Mon. Mag.* **92,** 207-11.

Crichton, M. I. & Campbell, W. D. (1949). Some records of *Ornithomyia fringillina* Curtis, with notes on its reproduction. *Ent. Mon. Mag.* **85,** 143-5.

O'Mahony, E. (1950). Ectoparasites from Fair Island. 2. *Ent. Mon. Mag.* **86,** 71.

Stansfield, G. (1955). Flat-fly infestation in the pipits and wheatears of Skokholm in 1954. *Bull. Fair Isle Bird Obs.* **2** (7), 318-20.

Thompson, G. B. (1938). The parasites of British birds and mammals. XIX. Further records of *Ornithomyia* spp. from British birds, together with notes. *Ent. Mon. Mag.* **74,** 129-33.

Thompson, G. B. (1940). The parasites of British birds and mammals. XXII. Additional records of *Ornithomyia* spp. from British birds, together with notes. *Ent. Mon. Mag.* **76,** 113-16.

Thompson, G. B. (1954). Contributions towards a study of the ectoparasites of British birds and mammals. No. 2. *Ann. Mag. Nat. Hist.* (12) **7,** 17-39.

Thompson, G. B. (1955). The parasites of British birds and mammals. XXVIII. Records of *Ornithomyia* spp. (Dipt., Hippoboscidae) collected during 1952. *Ent. Mon. Mag.* **91,** 4-5.

Williamson, K. (1951). The nesting of wheatears in 1951. *Bull. Fair Isle Bird Obs.* **1** (3), 31-3.

Williamson, K. (1954). The Fair Isle apparatus for collecting bird ectoparasites. *Brit. Birds,* **47,** 234-5.

Williamson, K. & Butterfield, A. (1952). Direct wheatear passage in August 1951. *Bull. Fair Isle Bird Obs.* **1** (6), 23-6.

THE FOOD AND FEEDING BEHAVIOUR OF THE JACKDAW, ROOK AND CARRION CROW

By J. D. LOCKIE

Edward Grey Institute, Oxford, and The Nature Conservancy, Edinburgh

(With 1 Figure in the Text)

This paper describes some aspects of the food and feeding behaviour of adult jackdaws *Corvus monedula*, rooks *Corvus frugilegus* and carrion crows *Corvus corone*. The study area, consisting of about 60 square miles of mixed farmland, pasture, parkland and woodland has, as its centre, the University estate at Wytham 3 miles west of Oxford. All three species of corvid are common in the area. The work was done while holding a Nature Conservancy Post-Graduate Research Studentship at the Edward Grey Institute, Oxford. Dr D. Lack, F.R.S., supervised the research and D. F. Owen helped with some of the field-work. The following checked my identification of or initially identified the animals obtained from gizzards: D. F. Owen (Lepidoptera), Professor L. W. Grensted (Diptera), M. J. Davies (Coleoptera), M. Williamson (Gastropoda) and H. F. D. Elder (seeds). The farmers, Messrs. Wise, Cornish and Lane, gave unrestricted access to their respective farms. Dr Bruce Campbell kindly delivered corvid corpses, often within a few hours of their having been shot.

FOOD EATEN AS DETERMINED BY GIZZARD ANALYSIS

A small number of rooks, jackdaws and carrion crows were shot by myself each month from September 1951 until May 1953 around Oxford. The gizzards were immediately opened and the contents placed in 70% alcohol or 5% formalin. Some birds were also accepted from a reliable gamekeeper who gave details of when and where each bird was obtained and who poured 5% formalin down the gullet of the shot bird in order to arrest digestion. The birds were then delivered to me as quickly as possible. Most rooks and jackdaws were shot soon after entering a roost in the evening and the rest on farmland. The similarity of the contents of each gizzard collected in a particular month suggests that, for these species, a moderate sample of birds is sufficient to give adequate information.

Gizzard contents were later poured into a large white dish and the obvious animal remains picked out by hand. Stones were then removed and search made for the head capsules of leatherjackets. The vegetable matter remaining was identified as far as possible, dried of surface moisture on blotting paper, and the volume measured by the displacement of water; husks of grain were included with grain. Some samples of the gritty residue were then examined under the microscope for earthworm chaetae. It was impracticable to examine the grit and other

Table 1. *Percentage of gizzards containing various animal foods: 1951-53*

\+ = present; — = not found.

JAN.-FEB.	Rook	Jackdaw	Carrion crow
Curculionidae, imagines	6	26	—
Diptera, imagines	—	6	—
Other insects	13	12	—
Gastropoda	6	35	+
Lumbricidae	75	—	+
Number of gizzards examined	16	34	1

The weevils which could be identified were *Sitona* sp. (probably *S. lineatus* (L.)) and *Barynotus obscurus* (Fabr.). The snails were *Hellicella* sp. and *Hygromia* sp. Diptera were *Scopeuma stercorarium* (L.) and *Borborus* sp.

MAR.-APR.			
Curculionidae, imagines	11	54	17
Coleoptera, imagines (other than Curculionidae)	28	29	58
Coleoptera, larvae	22	7	17
Lepidoptera, larvae and pupae	11	11	8
Other insects	17	18	33
Gastropoda	—	21	42
Lumbricidae	83	18	83
Carrion	6	—	33
Number of gizzards examined	18	28	12

Adult Coleoptera (apart from weevils) were *Agriotes sputator* (L.), *A. obscurus* (L.), *Harpalus* sp., and *Aphodius* sp. Larval Lepidoptera were *Celaena secalis* (L.) and *Leucania* sp. Other insects were mainly *Scopeuma stercorarium* (L.) and lycosid spiders.

MAY-JUNE			
Curculionidae, imagines	17	60	—
Coleoptera, imagines (others)	33	50	+
Coleoptera, larvae	17	10	—
Lepidoptera, larvae and pupae	17	20	—
Diptera larvae	33	10	—
Other insects	67	20	+
Gastropoda	—	20	+
Lumbricidae	100	—	+
Number of gizzards examined	6	10	2

Coleoptera (other than weevils) were *Agriotes* sp., *Harpalus* sp., *Sphaeridium scarabaeoides* (L.), *Cassida* sp. and *Byrrhus pilula* L. Lepidoptera were larval *Celaena secalis* (L.) and the larvae and pupae of *Hepialus lupulinus* (L.).

AUG.-OCT.			
Curculionidae, imagines	27	48	+
Coleoptera, imagines (others)	27	35	+
Lepidoptera, larvae and pupae	36	13	—
Diptera, imagines	45	26	—
Diptera, larvae and pupae	27	—	—
Arachnida	—	9	—
Other insects	9	13	+
Gastropoda	—	9	+
Lumbricidae	55	—	+
Number of gizzards examined	11	23	3

Adult Diptera were Tipulidae, *Scopeuma stercorarium* (L.) and *Polietes lardaria* (Fabr.). The weevils were *Sitona* sp., *Otiorrhynchus* sp. and *B. obscurus* (Fabr.). Other adult Coleoptera were *Aphodius rufipes* (L.), *A. erraticus* (L.), *A. ater* (Dg.) and *Amara* sp. Lepidoptera larvae (mostly found in rooks) were likely to have been *Triphaena pronuba* (L.).

NOV.-DEC.			
Curculionidae, imagines	18	20	—
Coleoptera, imagines (other than above)	18	—	+
Other insects	18	20	+
Lumbricidae	82	10	+
Carrion	—	—	+
Number of gizzards examined	22	10	3

debris for minute animal remains such as chelicerae of spiders, and so the occurrence of certain groups of small animals was perhaps underestimated.

Hartley (1948) has reviewed the many means by which the food of birds may be analysed. No method is ideal and it seems best to use that which will best elucidate the problem under consideration. The method adopted here is that of the percentage of gizzards containing each food; by this means earthworms, which are rarely found whole in the gizzards, can be included in the analysis. The method does, however, tend to emphasize similarities between the food of the different species.

In Table 1 the animal food of rooks, jackdaws and carrion crows is analysed in two-monthly periods. The notes to Table 1 give the species and genera of animals which could be identified. The remainder, a considerable number, were too macerated to allow identification below a family, or higher grouping; hence the broad groupings in Table 1.

The food obtained from the gizzards of rooks, jackdaws and carrion crows was varied. Nevertheless, some important differences are evident. Throughout the year, earthworms occurred in 80% of rooks (and also in carrion crows) but in only 6% of jackdaws. Twice as many rooks as jackdaws took coleopterous larvae and six times as many took dipterous larvae. On the other hand, 42% of jackdaws but only 1% of rooks contained snails. It is noteworthy that rooks tended to feed on animals which live below the surface in contrast to jackdaws. Carrion crows occupied an intermediate position in that they contained at some time, similar animals to those found in both rooks and jackdaws. The differences outlined above were most pronounced in January and February and, to a lesser extent, in May and June.

The percentages of animals selected from each of four length-groups by rooks, jackdaws and carrion crows are given in Table 2. In each corvid, the length of

Table 2. *Body-length of animals selected as food by jackdaw, rook and carrion crow*

Figures show the percentage of animals taken from each length-group. Lengths were obtained either by direct measurement or from the literature as an average for the species. Only Coleoptera, Diptera, Lepidoptera and Gastropoda are included.

	Jackdaw	Rook	Carrion crow
2- 6 mm	41	21	16
7-12 mm	34	31	51
13-18 mm	24	31	22
19 mm and over	1	17	11
Total number of gizzards	105	76	21
Total number of animals	298	130	67

animal taken as food varied greatly but the rooks took fewer animals in the smallest size-group than the jackdaw and more in the largest. The animals taken by carrion crows were similar in length to those taken by rooks.

Table 3 shows the percentage of gizzards which contained various vegetable foods. Grain (barley, wheat and oats) occurred in almost every gizzard of rook and jackdaw in almost every month of the year. The source of this food changed

with the seasons. For example, observations on feeding flocks of rooks and jackdaws showed that in June and July grain was got from feeding troughs; standing crops were only raided in very dry weather in July. In autumn, most grain was obtained from stooks and stubble and later, to some extent, from drills. During winter the birds ate grain from feeding troughs and stacks and in March and April mostly from drills.

Table 3. *Percentage of gizzards containing vegetable foods*

The number of gizzards involved is given in Table 1. No samples were obtained in July. + = present; — = not found.

		Jan.-Feb.	Mar.-Apr.	May-June	Aug.-Oct.	Nov.-Dec.
Grain	Rook	94	100	83	100	100
	Jackdaw	89	89	80	100	90
	C. crow	—	83	+	100	66
Other farm produce	Rook	69	11	—	—	—
	Jackdaw	26	14	—	—	—
	C. crow	+	—	—	—	66
Weed seeds	Rook	13	—	—	—	5
	Jackdaw	35	18	—	17	20
	C. crow	—	8	—	—	—
Elder and plum	Rook	—	—	—	18	—
	Jackdaw	—	—	—	22	10
	C. crow	—	—	—	—	—
Acorn	Rook	—	—	—	9	5
	Jackdaw	—	—	—	13	—
	C. crow	—	—	—	—	—

Other farm produce eaten was mainly potatoes, beans and occasionally peas. In late autumn, rooks and jackdaws fed upon elderberries (*Sambucus nigra*), acorns, and locally, cultivated fruit. Small seeds were eaten in autumn and winter by jackdaws and, to a lesser extent, by rooks. The species of seed most often found was *Polygonum convolvulus* L.; the following seeds were recorded once, *Ranunculus acris* L., *Polygonum aviculare* L., *P. persicaria* L., *Trifolium pratense* L., *Atriplex* sp., *Vicia* sp. and *Cirsium* sp. Kluijver (1945) found that jackdaws in Holland contained animal and vegetable food similar to that described here.

FEEDING ACTIONS ON GRASSLAND

Observations on the feeding methods employed by the three species of corvid provide a check to certain conclusions drawn from gizzard analysis. Various feeding methods are employed; most are used by all three species but to different extents.

Jumping occurs when adult Diptera are particularly common on grassland, chiefly therefore in May, June, August, September and October. The jumps are often spectacular; this method of feeding is illustrated in Fig. 1*a*. Jackdaws, rooks and carrion crows jump for Diptera but there is no doubt that the lightly built jackdaw is far the most efficient of the three at catching adult Diptera in flight. One jackdaw, watched at close quarters, ran through the grass from cow-pat to cow-pat. As it approached a pat it ran faster half-opening its wings to aid speed and leaped upon the Diptera which were crowded upon the dung. The bird usually

managed five or six snaps before the flies dispersed. A variation is sometimes seen; the jackdaw flies over the grass at about 15 ft and drops vertically on to the cow-pat snapping right and left. Podmore (1948) describes this method of feeding in jackdaws.

Pecking requires no explanation, the food merely being lifted from the surface. All three species use this method.

Surface-probing is illustrated in Fig. 1*b*. The bill is pushed into the tuft of grass and opened, thus parting the blades and stems and exposing animals otherwise invisible. Alternatively, the bill is kept closed and used as a lever to lay the stems to one side. The method is used by all three species.

Fig. 1. The feeding actions of the rook on grassland: *a*, jumping; *b*, surface probing; *c*, deep-probing; *d*, pouncing

Clod-turning consists of turning over any object on the ground, a clod of earth, a piece of wood, or dry dung. All three species use this method.

Deep-probing is shown in Fig. 1*c*. The bill is pushed into the holes which large leatherjackets and certain species of earthworm make in the soil. The mandibles are then opened, thereby enlarging the hole. Lorenz (1949) has described this method of feeding in the starling (*Sturnus vulgaris*). I have often seen rooks probe in this manner into the centre of a worm cast. Newstead (1908) observed rooks feeding on the short turf of a golf course. The rooks probed in the burrows made by fully-fed leatherjackets which were very abundant. Newstead states that the rooks had difficulty in dislodging the larvae and often had to dig them out (see 'Digging'). Although jackdaws and carrion crows attempt deep-probing they seem to perform it less efficiently than the rook; the carrion crow is, however, more efficient than the jackdaw, probably on account of its longer bill. Jackdaws will certainly eat earthworms when they can get them but, except during ploughing, earthworms seem largely unavailable to jackdaws.

Digging occurs in hard ground when probing is difficult; earthworm burrows may also be excavated. The burrow may be enlarged by deep-probing or by using the closed bill as a lever. Sharp blows are given to the walls of the hole and the dislodged earth is tossed aside. One bird which I disturbed after watching it digging, had excavated a conical hole 2 in. in diameter and 3 in. deep; an earthworm burrow

disappeared into the ground at the apex of the hole. Rooks often dig in cow-pats but often the cow-pat is scattered rather than dug into; the method of feeding is then similar to clod-turning. Jackdaws and carrion crows were rarely seen to dig in the ground although both species scatter cow-pats. Jackdaws are more or less limited to the old dry cow-pats for feeding, as they seem unable to deal with the soft sticky dung of those recently deposited. Several times I have seen a jackdaw move to a fresh cow-pat, which had just been opened and scattered by a rook, and search for food.

Pouncing has not been seen on many occasions and then only in the rook and carrion crow. The prey on every occasion noted was an earthworm. The feeding bird, walking through the grass, suddenly pounces and drives its bill vertically downwards; immediately the bird leans back, pulls steadily, and slowly draws the worm from its burrow (Fig. 1*d*).

Some foods can be swallowed straightway but others must first be prepared. In particular, the rook holds earthworms in one foot and with the bill tears them into several pieces (this makes the identification of undigested worms in the gizzards very difficult). Acorns, ears of grain and other large particles of food are also held in the feet and hammered into small pieces with the bill.

The percentages of the various feeding actions used by rooks and jackdaws in each month on grass, are shown in Table 4. The counts were made on grass fields used by both rooks and jackdaws; on many occasions mixed flocks were present. Observations were made with 10×50 binoculars only on birds which could be watched at fairly close range and in good light; this enabled me to assign all the feeding actions to one or other of the categories already described. The method used was to choose any feeding bird, watch it closely for up to five feeding actions, then move to another bird and repeat the observations. In general, the conclusion drawn from the analysis of gizzard contents, that rooks and jackdaws eat different foods, is corroborated. Jackdaws obtained their food mainly by jumping, picking, surface-probing and clod-turning; rooks mainly used deep-probing, digging and pouncing though many of them used the methods preferred by the jackdaw.

Rooks and jackdaws tend to feed in different niches, but overlap considerably. While, however, the rook feeds to some extent upon the animals which live in the feeding niche of the jackdaw, the jackdaw does not exploit the animals in the niche of the rook to the same extent. For example, rooks fed mainly on the surface in October and below the surface in December, February and June, whereas jackdaws fed mainly on the surface in all months.

Gizzard analysis is not a wholly satisfactory means of assessing the food of most birds, since some foods are digested more quickly than others (see van Koersveld 1951, for a discussion of this problem in jackdaws). However, by using counts of feeding actions and the results of sampling the feeding habitat, an estimate of the relative proportion of certain animals eaten by the rook can be made. For this purpose, jumping, picking and surface-probing are grouped, since these three actions are directed to objects on the surface. Similarly, deep-probing, digging and pouncing are grouped since these are directed to objects below the surface. Clod-

Table 4. *Relative frequency (%) of the feeding actions used by rooks and jackdaws on grassland near Oxford*

		1952					1953					
		Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Jumping	Rooks	0	5	10	2	0	0	0	0	0	—	3
	Jackdaws	16	14	34	10	5	0	3	0	10	—	9
Picking	Rooks	27	51	53	24	15	15	13	42	57	—	28
	Jackdaws	53	61	48	44	25	47	61	30	70	—	47
Clod-turning	Rooks	2	6	5	6	8	7	9	5	4	—	0
	Jackdaws	5	17	11	24	38	13	14	42	16	—	19
Surface-probing	Rooks	23	4	17	30	15	33	0	7	4	—	0
	Jackdaws	22	5	6	20	25	33	19	16	2	—	25
Deep-probing	Rooks	23	8	8	33	52	41	26	27	14	—	25
	Jackdaws	2	0	1	2	7	0	0	12	2	—	0
Digging	Rooks	25	26	7	5	10	0	17	4	7	—	42
	Jackdaws	2	3	0	0	0	7	3	0	0	—	0
Pouncing	Rooks	0	0	0	0	0	4	35	15	14	—	2
	Jackdaws	0	0	0	0	0	0	0	0	0	—	0
Number of observations	Rooks	52	117	124	63	40	27	23	55	28	—	40
	Jackdaws	68	59	160	99	40	15	70	79	50	—	32

turning I have excluded. The average weight of animals on, and below the surface respectively, was obtained from animals collected by sampling permanent pasture (Lockie 1955). From September to December 1952, earthworms were the most abundant animals living below the surface and which were suitable for rooks. By multiplying the number of feeding actions directed to objects in each niche by the average weight of animals in that niche, the relative weight of animals removed by rooks from the surface and from below the surface was calculated. Measured in this way, the percentage weight of earthworms in the animal food obtained by rooks from grassland at Oxford in 1952 was, in September 55%, October 65%, November 95% and December 97%. The food of nestling rooks supports this finding. The technique used to obtain food from nestlings allowed the animals to be secured wholly undigested and earthworms were found to form the bulk of the food (Lockie 1955). This shows how misleading the macroscopic analysis of gizzard contents alone may be. Earthworms are the very food that the most recent previous survey of rook food had to ignore since the numbers or volume could not be measured (Fisher 1948). Similarly Campbell (1936) concluded from the analysis of gizzards that the food eaten by rooks and jackdaws in the south of England was almost identical. He did not, however, look for earthworm remains.

SUMMARY

1. The analysis of food from gizzards shows that rooks and jackdaws tend to eat different kinds of animals. Carrion crows eat the same kinds of animals as are eaten by rooks and jackdaws and, in addition, other prey. Grain is eaten by all three species but only jackdaws eat weed seeds to an appreciable extent. The differences in diet are most pronounced in mid-winter and least so from April to June and in Autumn.

2. The feeding methods used on grassland are described and the relative proportion of each used by rooks and jackdaws given. These observations corroborate the conclusions drawn from a microscopic analysis of gizzard contents.

REFERENCES

Campbell, J. W. (**1936**). On the food of some British birds. *Brit. Birds*, **30,** 209-18.
Fisher, J. (**1948**). Rook Investigation. *Agriculture, Lond.* **55,** 20-3.
Hartley, P. H. T. (**1948**). The assessment of the food of birds. *Ibis*, **90,** 361-81.
Kluijver, H. N. (**1945**). Eenige gegevens over het voedsel en economische beteekenis van de Kauw (*Coleus monedula*). *Limosa*, **18,** 1-11.
Koersveld, E. van (**1951**). Difficulties in stomach analysis. *Proc. Xth Int. Orn. Congr.* (1950). 592-4.
Lockie, J. D. (**1955**). The breeding and feeding of jackdaws and rooks with notes on carrion crows and other Corvidae. *Ibis*, **97,** 341-69.
Lorenz, K. Z. (**1949**). Ueber die Beziehungen zwischen Kopfform und Zirkelbewegung bei Sturniden und Iktiriden. In **Mayr, E. & Schüz, E.** *Ornithologie als biologische Wissenschaft.* Heidelberg. Pp. 153-7.
Newstead, R. (**1908**). The food of some British wild birds. *J. Bd. Agric.* (Suppl.) **15,** 53-6.
Podmore, R. E. (**1948**). Jackdaws hawking insects. *Brit. Birds*, **41,** 272.

A BOTTOM SAMPLER FOR INCLINED ROCK SURFACES IN LAKES

By J. H. MUNDIE*
Imperial College, London

(With Plate 2, and 1 Figure in the Text)

In the quantitative sampling of animals or plants living on the floors of lakes a difficult problem is presented by inclined rock surfaces for these cannot be sampled by grabs or corers. Krecker & Lancaster (1933) sampled shelving rock down to a depth of 6 ft by scraping with a dip net or by lifting rocks with a grapple. This can only be done in shallow water, however, and is, moreover, likely to result in loss of material.

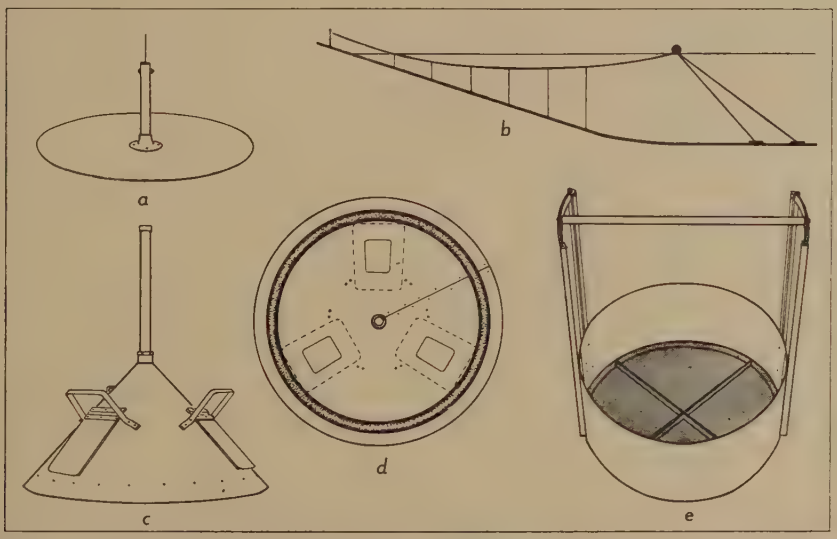


Fig. 1. *a*, Plate with pipe fitting; *b*, layout of plates on the side of the reservoir showing the line and the retrieving wires of 6 plates; *c*, cone with flap-valves; *d*, cone from below; *e*, bucket. For details see text.

In a recent survey of the Chironomidae of storage reservoirs (Mundie, in press) a very similar problem arose. The sides of one reservoir had a slope of 1 in 3 and consisted of concrete slabs covered with *Cladophora* or with a thin layer of sediment and lying below 1-5 m of water. The following apparatus was devised to sample these. It worked satisfactorily, with certain limitations, and is offered as one approach to this sampling problem.

The principle of the method is to put down a false bottom, allow material to

* Now at the Freshwater Biological Association, The Ferry House, Ambleside.

settle on it in the course of some weeks, and animals to migrate on to it, and then to lift it. Moon (1935) has discussed its use in lakes. The obvious disadvantage is that some time must elapse before samples can be taken.

The false bottom consists of a plate of asbestos-cement composition. This material was chosen because it is chemically inert, similar in texture to concrete, and readily procurable. The plate (Fig. 1*a*) is rimless and so offers no barrier to wandering animals. It is 3 mm thick and 41 cm in diameter. Attached to its centre by a short flanged pipe threaded internally is a duralumin tube 1·9 cm in diameter and filled with lead to give greater weight. The upper end of this is about 15 cm from the plate. A brass bolt is passed through it to secure a copper retrieving wire. The other end of this wire is tied to a horizontal line laid out on the water.

The line (Fig. 1*b*) is of lubricated pregalvanized steel wire rope 4·76 mm ($\frac{3}{16}$ in.) in diameter and 25 m long. It is shackled to an iron post on the shore and secured at its other end to a swivel-piece below a large buoy moored by two cables. Large boiler plates may be used for anchors. The line is kept fairly taut by being tightened from the shore. Several plates are set out with their retrieving wires tied to the line as shown in Fig. 1*b*. The wires are about 2 m longer than the depth of water in which the plates are laid so that if the line is displaced laterally when sampling is being done, the plates are not disturbed.

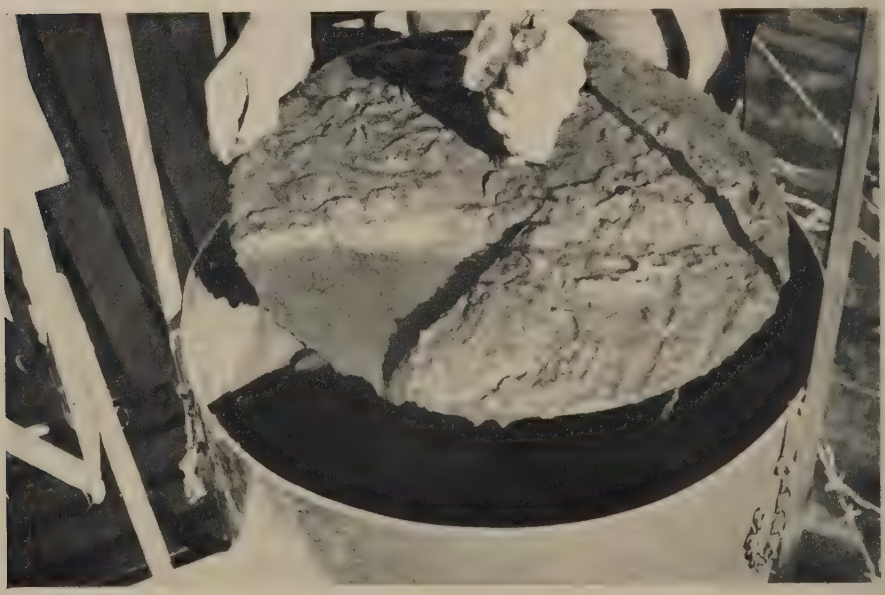
The plates were set out on the side of the reservoir at each metre depth-zone and were therefore 3 m apart. It was found that it was not always possible to set plates at exact depths as they tended to slide downwards. Once they had come to rest, however, they remained secure.

It is probable that 4 weeks or even a shorter time are sufficient for the plates to assume the conditions of their immediate surroundings. Moon (1935) found that trays set in the littoral of Windermere were fully colonized in 4 weeks. All the plates used in the reservoir were at least 3 months old on being lifted. By that time they were indistinguishable from their surroundings, for on calm sunny days when the bottom was visible all that could be seen of them were the pipes projecting above the substratum.

To lift plates without loss of the material on them the apparatus shown in Fig. 1*c* and *d* was used. It consists of a cone of aluminium (1·98 mm thick) 45 cm in diameter and 22 cm high and fitted with three flap valves also of aluminium. The seating for each flap is beaten flat and a broad rectangular rubber washer is stuck to it with adhesive compound (broken line in Fig. 1*d*). The hinges are also of rubber. Inside the cone near the base a rubber tube 15·9 mm (5/8 in.) in diameter is secured by a series of small screws and nuts. The heads of the screws are inside the tube. The ends of the tube are sealed together so that it remains air-filled. Through the apex of the cone passes a duralumin pipe 30 cm long, 4 cm of which are within the cone. Three brass brackets bolted to the outside of the cone serve as handles.

When a plate is to be lifted the line is passed over the rowlocks of the boat to hold the boat in position. The retrieving wire is untied from the line and then

A. A plate from 1 m with sector removed to show the thickness of the bottom material.



B A plate from 4 m.

passed through the cone from below upwards. The wire is held fairly taut and the cone released. It falls slowly and vertically, the flap valves opening during the descent. When the cone comes to rest on the plate the valves close under their own weight and both plate and cone can be raised by a steady pull on the wire. The rubber tube inside acts as a seal round the periphery of the plate.

The ascent is stopped as soon as the pipe at the apex reaches the water surface. If the apparatus is suddenly lifted out of the water at this stage the valves open and water passes out of the cone carrying bottom material with it. To prevent loss a large bucket (Fig. 1*e*) 50 cm in diameter, 23 cm high and with a gauze bottom (aperture 0·25 mm, 60 meshes per linear inch) is passed under the cone and plate while they are in the water and all are lifted out slowly. The floor of the bucket has cross bars to take the weight.

As a safety measure during sampling a long light cord is tied to one of the brackets so that the cone can be recovered should the wire break.

Two plates, freshly lifted, with sectors removed to show the depth of the deposits are shown in Plate 2; *A* is from 1 m of water and *B* from 4 m.

When the plates were lifted from the reservoir very little material was found to be washed into the bucket. Each sample was transferred via a large metal funnel to a labelled jar. To do this the plate had to be scraped with a stiff rubber scraper and washed.

One advantage of the method is that it is possible to see whether samples are satisfactory or not. If a plate is only partially covered with deposit the sample can be discarded.

The depth of material on the plates varied from 1-2 mm at less than 1 m of water to about 2 cm at 6 m. Below 5 m, however, it is not likely that the mud on the plate was equal in depth to that of its surroundings for the plate might be resting on stones. Consequently a depth of 5 m was taken as the limit to which the sampler could be used.

At depths less than 0·5 m, where wave action was strongest, the *Cladophora* was very securely attached to the plates and could be removed only by vigorous scraping. Here, therefore, plates could be lifted by hand without loss of material and this method of sampling can be regarded as entirely satisfactory, always provided that the plates are not interfered with by the public.

Apart from public interference (sometimes unintentional, as for example, when fishermen caught their hooks on the lines and vertical wires), certain other sources of error were found. One was movement of the boat on windy days which resulted in faulty sampling. Plates were therefore lifted only in calm weather. Another was failure of the cone to descend onto the plate. This could be due to a kink on the wire, to growth of *Cladophora* on it, or to the presence of the mollusc *Dreissena polymorpha*. In summer, therefore, plates can be left on the bottom too long. Yet another source of error was the entanglement of the vertical wires of two neighbouring plates which had been set too close together.

The samples were used mainly for faunistic counts. The area of each plate was taken at 0·125 m^2 and it was considered unnecessary to make allowance for the

pipe fitting or the area at the periphery with which the rubber tube makes contact.

The plate shown in Pl. 2, *A* yielded 5800 chironomid larvae, while plate (*B*) yielded 2000. Consequently a sample from a rich habitat presents a most laborious sorting task and it may be necessary to take a sub-sample of the material. This is most conveniently done by dividing up the sample whilst it is still on the plate.

This work was part of an investigation carried out on the reservoirs of the Metropolitan Water Board whilst I was in receipt of a maintenance grant from the Nature Conservancy. Full acknowledgment of the substantial assistance I received throughout the investigation is given in my paper in the press. Specific to the present paper are my best thanks to Mr J. S. Porter for help in making the apparatus and to Mr J. W. Siddorn for taking the photographs.

REFERENCES

Krecker, F. H. & Lancaster, L. Y. (1933). Bottom shore fauna of western Lake Erie; a population study to a depth of six feet. *Ecology*, **14**, 79-93.

Moon, H. P. (1935). Methods and apparatus suitable for an investigation of the littoral region of oligotrophic lakes. *Int. Rev. Hydrobiol.* **32**, 319-33.

Mundie, J. H. (in press). The ecology of Chironomidae in storage reservoirs. *Trans. R. Ent. Soc., Lond.*

REVIEWS

THE BIOLOGY OF *GLOSSINA*

P. A. Buxton (1955). *The Natural History of Tsetse Flies.* Pp. viii+816; 47 plates; 165 text-figures. London: H. K. Lewis (London School of Hygiene and Tropical Medicine, Memoir No. 10). Price 84*s*.

Trypanosomiasis in man and animals in Africa is still of great economic importance. Human sleeping sickness has frequently given rise to devastating epidemics. Anima. trypanosomiasis has made it impossible to keep cattle or horses over vast areas. The parasites causing these diseases are carried by tsetse flies and by no other vectors (except perhaps for occasional mechanical transmission by other biting insects). Research in many parts of Africa and elsewhere over the last fifty years has given many important results of practical importance in the treatment of human and animal trypanosomiasis and in the control of the tsetse fly, and this authorative and up-to-date summary will be of great value to medical and public health administrators as well as to research workers concerned with these problems.

This book is also, however, an important contribution to ecology. No other insect, and few other animals, have received the detailed study which has been devoted to the tsetse fly. (Professor Buxton has shown that it is legitimate to talk about 'the tsetse fly; the genus *Glossina* contains 21 species and some dozen subspecies, but the differences between the various forms are small and all have very similar life histories and habits'.) One might expect the study of this insect to prove comparatively simple, for the tsetse fly has a life history which appears at first sight to be much less complicated than that of almost any other insect. The only active, free-living stage is the adult, for the egg hatches inside the mother and the whole larval period is spent in the same situation. The female produces only one young (i.e. one larva which is ready to pupate) at a time, and the rate of reproduction is slower than that of some mammals. The only food of both sexes is vertebrate blood. The genus is restricted in its distribution to the comparatively narrow range of climatic conditions found in the tropics and subtropics, and does not extend to upland areas within these regions where temperatures approach those of temperate zones. Yet after reading this book one realizes that, notwithstanding the real advances which have been made, the fundamental explanation of many problems in the ecology of the tsetse fly still elude us. The work under review enables the reader to obtain a general picture of the tsetse fly in a way not previously possible. There has been a tendency for investigators in one area to concentrate on the problem as it appears in that area; it is now shown how results from one part of Africa may help in the understanding of the problem in another.

A full account of the anatomy of all described species and subspecies is given, with keys for their identification. Maps showing the distribution of most species are included. Buxton considered that the single non-African record for this genus, of *G. tachinoides* in Arabia, is authentic. The physiology of the insect is fully described, together with an account of laboratory experiments on behaviour. A long chapter entitled 'Movement and rest' deals with migration and movement in the field. The effects of climatic factors, particularly temperature and humidity, are described, and the correlations between laboratory and field work are discussed. Gaps in our knowledge here, where Buxton himself had initiated much of the later work, are stressed; throughout the book useful suggestions for future research abound. Tsetse are intimately concerned with the type

of vegetation in any area, and this question is dealt with at some length; the section entitled 'Botanical background' summarizes in some sixteen pages an immense amount of information which should be of very general interest even to those with little concern for medical entomology. The sexual physiology of the genus, including the biology of the larva and the pupa, is fully described.

In the chapter entitled 'Causes of death' the regulation of numbers is considered. In most species of animals, the amount of food available is believed to be one of the most important factors determining the number of individuals which occur in any area. With tsetse and to a lesser extent with other blood-sucking insects generally (for most others either as larvae or adults have additional sources of food) the situation is different. If there are sufficient hosts to nourish any flies at all, then there are enough to nourish either a large or a small population. The only exception is when the flies become so numerous as to drive away potential hosts; there are few if any authentic instances of this happening to a degree likely to reduce the food supply in a significant way. Excessive heat certainly wipes out flies in some areas, and cold weather prevents activity. There has been much good statistical work done on the results of field collections, and their correlation with weather and other conditions. It has been found, for instance, that it is possible to relate population changes in a complex way positively with soil temperatures at a depth of one foot two months before a given date, and negatively with annual rainfall, but these factors clearly do not directly control tsetse numbers, and must only be closely correlated with some unknown factors which are biologically effective. After analysing all factors influencing longevity, Buxton concludes: 'It is difficult to see what factors may be responsible for regulating populations of *Glossina*. Unfavourable conditions of climate are presumably independent of density and cannot regulate it. Competition for blood between individual tsetse flies does not, we believe, take place. We are left to suppose that the "enemies" (using the word broadly) of the fly or the puparium must be responsible for the regulation. But it must be admitted that we have no evidence that any enemy becomes more numerous or more effective at higher densities of tsetse population. We have indeed very little knowledge of the causes or mechanisms which prevent an indefinite increase of these insects when external conditions are favourable, but one must certainly suppose some such factor exists.' It would perhaps be salutory for all ecologists to read this section, particularly when they begin to imagine that they have 'solved' a problem!

KENNETH MELLANBY

PREDATOR-PREY RELATIONS

Thomas G. Scott and Willard D. Klimstra (1955). *Red Foxes and a Declining Prey Population.* Pp. 123; 14 text-figures. Carbondale, Ill.: Southern Illinois University Press (Monograph Series No. 1). Price $2.00.

The current scarcity of rabbits is unusual for the British Isles, but foxes in North America experience a scarcity of mammalian prey at fairly frequent intervals. The present study gives an account of the feeding habits of foxes during a three-year period of declining numbers of cottontail rabbits, meadow mice, white-footed mice, bob-white quail and other animals, including four species of snakes. Bob-whites and snakes formed a very small part of the diet of the foxes, and the authors conclude that predation alone is unlikely to have brought about the scarcity of these or the other species. The scarcity affected a wide area in the north-central states.

There was little year-to-year change in the relative frequency of the various items in the fox droppings, but a well marked seasonal change in the occurrence of vertebrate remains when insects and fruit became available. Foxes evidently found less to eat when prey was scarce, as they left fewer droppings and uneaten food, were less selective and may have been unable to raise all their cubs. Only one family was present each year

on an area of 2620 acres, but the results of this intensive study agree with those from more extensive surveys in previous years.

The authors conclude that, within limits, foxes took the food that was most readily available. It is perhaps lucky that the prey populations all decreased at the same time, since methods of measuring so many trends were necessarily rough, and gave only limited information about the proportion of the prey populations eaten by foxes. It might have been harder to determine the influence of predation upon a prey species that became scarce after the rest; but the present study shows that such declines may occur for reasons apparently unconnected with the intensity of predation by foxes, a fact that should be borne in mind when interpreting the more complicated cases of asynchronous declines in prey populations.

The present study is a valuable account of a rather special instance of predator-prey relations, but also contributes a great deal to the more general aspects of this difficult problem.

DENNIS CHITTY

MAN AND HIS ENVIRONMENT

J. B. Cragg and N. W. Pirie (editors) (**1955**). *The Numbers of Man and Animals*. Pp. viii + 152; 1 plate; 10 text-figures. Edinburgh and London: Oliver & Boyd (for the Institute of Biology). Price 15*s*.

This book contains the papers read and the discussion which followed each at a symposium held by the Institute of Biology in September 1954. The authors include economists, anthropologists and physiologists as well as ecologists and statisticians, so that the variety of view-point is wide. Indeed it is the wide differences between the approach of the various contributors that make the book so stimulating, and since they are all attempting to assess the human implications of what is known rather than to put forward closely argued theories, it is also extremely readable. This same variety of subject matter makes it impossible to summarize the book in terms of a set of general conclusions, but it is reassuring to find that Lord Boyd Orr in the last contribution ends on a note of optimism concerning the ability of the world's resources to provide for the human race. In the last sentence of the discussion on Lord Boyd Orr's paper Mr E. M. Nicholson remarked: 'I think all present must have been impressed by how much more one can learn from this comprehensive approach rather than by studying particular aspects in water-tight compartments', and we should be duly grateful to the Institute of Biology. The book is excellently produced and has indices to both authors and subjects.

H. C. GILSON

NORTH-AMERICAN MAMMALS

Randolph L. Peterson (**1955**). *North-American Moose*. Pp. xii + 280; 66 text-figures (19 photographs). Toronto: University of Toronto Press; London: Cumberlege. Price £5.

> 'An elk looked out of the pine forest,
> He snuffed up east, he snuffed down west,
> Stealthy and still.
> His mane and his antlers were heavy with snow—
> I drew an arrow across my bow,
> Stealthy and still.'

For 1400 years after the old Viking in Kingsley's *Hypatia* sang his song of the elk hunt, the bow and later the rifle have taken constant toll of the elk in Europe. For the last 400 years of that period, men of European stock have been shooting the same animal

under the name of moose in North America. Today in Europe, the author states, 'In the Scandinavian countries of Sweden and Norway, relatively high moose populations are being maintained in spite of comparatively dense settlement and heavy hunting'—almost 15 000 are stated to have been killed in Sweden in 1948. But from much of Europe the animal has completely disappeared. In the United States, it was apparently much more abundant formerly in the northern New England and western Great Lake states than it is today; in many of these regions it is practically extinct. Estimates by the U.S. Fish and Wildlife Service in various years from 1937 to 1948 give annual totals for the moose population ranging from about 12 000 to 17 000. In Canada, which includes the greatest portion of the moose range in North America, 'it seems conservative to estimate the present population of moose at something between 200 000 and 300 000'. Estimates of the numbers of moose in Alaska range from 30 000 to 60 000, the author considering that the number today is probably above the lower figure. The various methods by which these estimates have been reached are described in the chapter 'Population Studies'.

The present position of the moose, then, seems, all things considered, to be more satisfactory than might have been expected. Nevertheless, there is every need for continued vigilance, particularly as the evidence so far obtained suggests 'that the rate of reproduction of moose is quite low. All available records indicate that normally less than one-half of the adult cows (two years of age or older) produce calves each year.' Once the status of the populations and the carrying capacity of the different ranges are determined, the author considers that there are two major methods of practical management of the moose—control of human decimating factors on the one hand, and of the habitat on the other. Past management policies in North America have been largely restricted to the first, and much investigation is still required on both methods before it can be said that moose populations are being managed on a sound basis.

The foregoing review has been written from the conservation standpoint. The book deals, however, not only with that aspect but with the distribution, life history, anatomy, food, diseases and parasites and general behaviour and activities of the moose, and includes a bibliography of about 450 titles. The first comprehensive work of its kind on the North American moose (though even for these days rather an expensive one), it is likely long to remain an important source of information.

COLIN MATHESON

Tracy I. Storer and Lloyd P. Tevis, Jr. (1955). *California Grizzly.* Pp. xii + 335; 2 coloured plates and 36 half-tone figures. Berkeley and Los Angeles: University of California Press; London: Cambridge University Press. Price 56*s.* 6*d.*

The bear, *sensu lato*, seems to have possessed a peculiar fascination for man from the earliest times. From western Europe through Siberia to Japan, and thence across North America, among Greeks of the classic age no less than among modern Red Indians, bear legends and bear cults have persisted. All who, in our more sophisticated times, retain an interest, from whatever angle, in these animals, will find this book by two members of the staff of the University of California well worth reading.

The California grizzly, however, has been extinct for about forty years. So, although there is one chapter on the physical features and another on the habits of the animal, summarizing what has been recorded on these subjects, the book in general can be regarded as an ecological one, and therefore appropriate for review in this Journal, only in so far as man is viewed as a factor in the environment, influencing the bear and influenced by it in turn.

Man's influence on the grizzly was probably negligible until comparatively modern

times. The aborigines were few and poorly equipped with weapons as with other material belongings. It was not until the coming of the Spaniards that the human factor became an important influence in the life of the grizzlies; and, in the first instance, that influence was favourable to them. The new and abundant food supply provided by the great herds of cattle, horses and sheep, reared by the rancheros apparently resulted in a marked increase in the grizzly population which continued in some areas up to the first half of the nineteenth century. Thereafter, with the influx of thousands of American pioneers and hunters, the story is one of swift and uninterrupted decrease to final extinction.

The influence of the grizzly on man was at its strongest among the aboriginal Indians, who had a large body of superstitions about the animal. The grizzly rather than man was the dominant organism of the region, and regarded with fear and awe, whereas the Black Bear was hunted for its flesh and pelt with impunity. The chapter on 'Grizzlies and Indians' contains much of interest to the anthropologist as well as to the zoologist. With the advent of the white men the grizzly, while still a dangerous foe, ceased to be the subject of awe and propitiation, though its influence on the imagination of the modern Californian is seen in two of the illustrations, showing the grizzly in a prominent position both in the official State Flag of California and in the Great Seal of the State.

The extensive bibliography, covering the zoological, historical and anthropological literature bearing on the grizzly, does not include one important paper that one might have expected to find there, Hallowell's 'Bear Ceremonialism in the Northern Hemisphere' (*American Anthropologist*, 1926, 1-175), in which there is much material of interest for comparative purposes though admittedly not a great deal about California.

COLIN MATHESON

BOOKS RECEIVED

The Invertebrates, Vol. IV. *Echinodermata*. By Libbie Henrietta Hyman. New York, Toronto and London: McGraw Hill. 1955. Price 75*s*.

Annual Review of Entomology, Vol. I, 1956. Edited by Ed. A. Steinhaus (and Ray F. Smith, Associate Editor). Stanford, Calif.: Annual Reviews Inc. 1956. Price $7.50.

Synökologie der Landtiere. By Wolfgang Tischler. Stuttgart: Fischer. 1955. Price DM. 36.00.

Kinship of Animals and Man: a textbook of animal biology. By Ann H. Morgan. New York, Toronto and London: McGraw Hill. 1955. Price 50*s*. 6*d*.

Ricerche sulla microfauna delle acque interne Ferraresi. By Mario F. Canella. Publ. del Civico Museo di Storia Naturale di Ferrara. IV, 1954.

Streams, Lakes, Ponds. By Robert E. Coker. Chapel Hill: University of North Carolina Press; London: Cumberlege. 1954. Price 48*s*.

Learning and Instinct in Animals. By W. H. Thorpe. London: Methuen. 1956. Price 55*s*.

Biologie der primär flügellosen Insekten. By J. Paclt. Jena: Fischer. 1956. Price DM. 27.00.

E. A. Birge: A Memoir. By G. C. Sellery with an appraisal of Birge the limnologist, *An Explorer of Lakes*, by C. H. Mortimer. Madison: University of Wisconsin Press. 1956. Price $3.50.

Peaceful Uses of Atomic Energy, Vol. 12. *Radioactive Isotopes and Ionizing Radiations in Agriculture, Physiology and Biochemistry*. New York: United Nations; London: H.M.S.O. 1956. Price 63*s*.

Dahlak. By G. Roghi and F. Baschieri. London: Kaye. 1956. Price 25*s*.

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. A. Allen, J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications . . .' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

PAGE

1. Ecological surveys and the relations of animals to habitat conditions 439
   (*a*) Marine and brackish 439
   (*b*) Fresh water 440
   (*c*) Land 441
2. Methods, apparatus, population statistics and taxonomic studies of use to ecologists 446
3. Parasites 448
4. Food and food habits 449
5. Migration, introductions and local distribution 451
6. Studies on behaviour 458
7. Reports of organizations 458

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Bagenal, T. B. (1955). The growth rate of the long rough dab *Hippoglossoides platessoides* (Fabr.). *J. Mar. Biol. Ass. U.K.* **34,** 297-311, 643-647 [a correction].
Includes comparison of growth rates of fish from the Clyde, Iceland and the Baltic.

Blackburn, M. (1956). Sonic scattering layers of heteropods. *Nature, Lond.* **177,** 374-375.
Suggested cause *Firoloida desmaresti* swarming for reproductive purposes over parts of continental shelf.

Crisp, D. J. & Davies, P. A. (1955). Observations *in vivo* on the breeding of *Elminius modestus* grown on glass slides. *J. Mar. Biol. Ass. U.K.* **34,** 357-380.
The breeding cycle of this barnacle is described, and the influence of various factors on reproduction is considered. *Elminius* can breed at any season, provided that the temperature does not fall below 6° C and the food supply is adequate.

Cushing, D. H. (1955). Production and a pelagic fishery. *Fish. Invest. Lond.* (2) **18** (7), i-vi, 1-104.
A comprehensive attempt to estimate biologically and statistically the whole of the ecological relationships comprised in a North Sea herring fishery. Reviewed in detail elsewhere in this journal.

Forster, G. R. (1955). Underwater observations on rocks off Stoke Point and Dartmouth. *J. Mar. Biol. Ass. U.K.* **34,** 197-199.
A description of the commonest sublittoral Algae and sessile animals found on rocks down to a maximum depth of 28 m.

Gamulin, T. & Hure, J. (1956). Spawning of the sardine at a definite time of day. *Nature, Lond.* **177,** 193-194.
Spawning in the evening, as in Californian sardine. Evidence of similar phenomena in other marine fish. Methods described with results.

Green, J. (1955). The fauna of Cefn Sidan and its wrecks. *Nature in Wales.* **1** (4), 170-171.
The wreck fauna is a poorer version of that found on a rocky shore, differing completely from the fauna of the surrounding sand.

Hunter, W. R. (1954). On animal ecology in the Garvelloch Islands. *Glasgow Nat.* **17,** 147-150.
The effects of limestone soils on the animal communities of a small archipelago in the Firth of Lorne.

Marshall, S. M. & Orr, A. P. (1955). On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation and excretion in adult and stage V *Calanus*. *J. Mar. Biol. Ass. U.K.* **34,** 495-529.
Cultures of diatoms and phytoflagellates grown with radio-active phosphorus (^{32}P) present were used in observations on filtering rates, effects of light, the size of organism filtered off and the choice of food. In an actively laying female much of the ^{32}P appears in the eggs.

Newell, G. E. (1954). Animal zones of the North Kent coast. *S.-East Nat.* **59,** 34-54.
An account of the origin and distribution of the intertidal sea-floor deposits in Whitstable Bay and of the animal associations characteristic of the main zones represented. These comprise shingle slope, bound shingle, sandy flats, shell and shell-gravel, and exposed London clay. Notes are given on the feeding habits of some of the animals discussed.

Smith, R. I. (1956). The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of *Nereis diversicolor*. *J. Mar. Biol. Ass. U.K.* **35,** 81-104.

The correlation between the distribution of this polychaete worm and the salinity of the interstitial water in the muds is described.

Southward, A. J. (1955). On the behaviour of barnacles. I. The relation of cirral and other activities to temperature. *J. Mar. Biol. Ass. U.K.* **34,** 403-422.

The range of temperatures over which the cirri were active, and the frequency of beat at different temperatures measured in five British intertidal species. Two species with a southern distribution had a more rapid beat at high temperatures, and continued active to much higher temperatures than the northern species *Balanus balanoides*, which showed greater activity at low temperatures.

Southward, A. J. (1955). On the behaviour of barnacles. II. The influence of habitat and tide-level on cirral activity. *J. Mar. Biol. Ass. U.K.* **34,** 423-433.

Differences observed in activity of animals from different levels appears to be related as much to differences in growth-rates or general metabolic rates as to any adaptation to temperature conditions at each level.

Southward, A. J. & Crisp, D. J. (1956). Fluctuations in the distribution and abundance of intertidal barnacles. *J. Mar. Biol. Ass. U.K.* **35,** 211-229.

Fluctuation in the abundance of *Balanus balanoides* and *Chthamalus stellatus* may be explained by changes in the environment which favour one species or the other.

Southward, A. J. & Dodd, J. M. (1956). Studies on the biology of limpets. I. The late J. H. Orton's work on *Patella*. *J. Mar. Biol. Ass. U.K.* **35,** 145-147.

Orton, J. H., Southward, A. J. & Dodd, D. M. (1956). Studies on the biology of limpets. II. The breeding of *Patella vulgata* L. in Britain. *J. Mar. Biol. Ass. U.K.* **35,** 149-176.

Observations on breeding from six localities in Britain over a period of five years. *P. vulgata* is a winter breeder in Britain ; the time of spawning appearing to be correlated with rough seas and inshore winds.

Wilson, D. P. (1955). The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny. *J. Mar. Biol. Ass. U.K.* **34,** 531-543.

The importance of micro-organisms on the surface of sand grains as a factor affecting the settlement of this polychaete worm is demonstrated.

(*b*) Fresh Water

Healy, A. (1954). Perch (*Perca fluviatilis* L.) in three Irish lakes. *Sci. Proc. R. Dublin Soc.* (N. S.) **26,** 397-407.

A comparative study of perch in Barnagrow Lake, Lough Glore and Lough Rea. Growth was slower in Barnagrow Lake than in the loughs, but faster in all three than in the other British and continental waters investigated to date. There were differences in dominant year-classes between the lakes.

Popham, E. J. (1952). Some preliminary notes on the fauna Hygropetrica of Lancashire and the Isle of Man. *J. Soc. Brit. Ent.* **4,** 59-63.

The fauna hygropetrica is defined as those animals found on vertical or semi-vertical surfaces over which flows a film of water. The commonest species are the nematoceran fly *Thaumalea testacea* and the trichopteran *Tinodes assimilis* which replaces it where the water flow becomes more rapid.

Pyman, G. A. (1956). Hanningfield Reservoir: notes on the flooding of the reservoir and its effect on the ornithology of the area. *Essex Bird Rep.* **1955,** 50-51.

Notes on the effects of the gradual flooding of this new reservoir near Chelmsford from December 1954 to June 1955, followed by a recession of the water owing to the dry summer, lasting till December 1955.

Twomey, E. (1956). Pollan of Lough Erne. *Irish Nat. J.* **12,** 14-17.

Biological data for *Coregonus altior*, including age and growth, weight and food.

(*c*) LAND

Allen, A. A. (**1955**). *Conopalpus testaceus* Oliv. (Col., Melandryidae) and other Heteromera attracted to light. *Ent. Mon. Mag.* **91,** 198.

This beetle, which does not habitually visit light, was attracted to it in July in East Sussex. *Prionychus ater* and *Tenebrio molitor* have also been taken at light.

Allison, R. M. (**1956**). Failure of enforced hibernation to inhibit breeding in the frog (*Rana temporaria*). *Nature, Lond.* **17,** 342.

Frogs kept at 38 degrees F., four pairs spawned 7½ months later in mid May. Light and warmth kept at minimum. Breeding was delayed in some.

Anonymous (**1956**). Interaction of spray programmes and insect populations. *Nature, Lond.*, **176,** 902-904.

The mite *Metatetranchyus ulmi* has become a serious pest in the last thirty years, perhaps owing to side-effects of insect sprays. A comparison is given with respect to about 100 species dependent in varying degrees on *M. ulmi* of sprayed and derelict orchards. In sprayed the only serious predator seems to be *Blepharidopterus angulata*. Spray programmes should be altered to allow the establishment of several predators early in the season.

Banks, C. J. (**1954**). Random and non-random distributions of Coccinellidae. *J. Soc. Brit. Ent.* **4,** 211-215.

Aggregations are associated with hibernation during the winter, but in the spring are probably caused by mating pairs or due to chance.

Burnett, G. F. (**1956**). Variation in mortality with differences in humidity among mosquitoes exposed to BHC, Dieldrin and DDT. *Nature, Lond.* **177,** 663-664.

Seasonal effect of BHC and Dieldrin on females increasing at onset of the rainy season. Not noted with DDT. Suspected relationship with atmospheric humidity.

Burton, J. L. (**1956**). Report on the national census of heronries 1954. *Bird Study,* **3,** 42-73.

Records 6225 occupied nests in 520 heronries; 1% of English nests were not in trees, but in Scotland 10%. The index of heron population was 108 on the new standard, 4% above that of 1953 and 12% over the 1928 figure.

Chambers, V. H. (**1952**). The natural history of some *Pamphilius* species (Hym., Pamphiliidae). *Trans. Soc. Brit. Ent.* **11** (5), 125-140.

Species are better identified by type of abode in a rolled up leaf than by detailed descriptions of the larvae. Notes on food plants, dates of emergence, etc. are given.

Collingwood, C. A. & Satchell, J. E. (**1956**). The ants of the south Lake district. *J. Soc. Brit. Ent.* **5,** 159-164.

Records only seventeen species, this poverty being regarded as correlated with high rainfall. Discusses and tabulates relative abundance of species in closed and open canopy woodlands, sheep pastures, *Molinia* mosses and coastal areas, and also briefly, in relation to soil characters and altitude.

Colyer, C. N. (**1954**). The 'coffin' fly, *Conicera tibialis* Schmitz (Dipt., Phoridae). *J. Soc. Brit. Ent.* **4,** 203-206.

Discusses how these flies gain access to coffins.

Colyer, C. N. (**1954**). 'Swarming' of Phoridae (Diptera). *J. Soc. Brit. Ent.* **5,** 22-27.

Discusses five cases of indoor swarming.

Coulson, J. C. & White, E. (**1956**). A study of colonies of the kittiwake *Rissa tridactyla* (L.). *Ibis,* **98,** 63-79.

The history of a group of colonies in an area first colonized in 1930. Birds are present on sites of new colonies the year before breeding commences. Return to colonies and breeding are earliest in the oldest, latest in the youngest colonies.

Crowson, R. A. & Crowson, E. A. (**1955**). Some observations on beetles of the family Clambidae. *Glasgow Nat.* **17,** 205-206.

Includes notes on food and breeding biology.

Davies, L. (1955). Behaviour of young and old females of the black-fly *Simulium ornatum* Mg. *Nature, Lond.* **176,** 979-980.

Fat content is a valuable guide to age. Old flies bite frequently in late evening, and apparently about twice as often as the young.

Dempster, J. P. (1955). Factors influencing small-scale movements of some British grasshoppers. *Proc. R. Ent. Soc. Lond.* (A) **30,** 145-150.

Nymphs and adult males of *Chorthippus parallelus* tend to move from short to long vegetation, while adult females show the reverse tendency. Experiments with *C. brunneus* give essentially the same results except that adult females showed no tendency for differential movement.

Dove, R. S. (1956). Birds in and about a Ballymena plantation. *Irish Nat. J.* **12,** 2-10.

The results, presented as an annotated systematic list, of a ringing and colour-marking scheme operated in a small mixed plantation on the outskirts of Ballymena, Co. Antrim.

Duffey, E. (1955). *Lepthyphantes whymperi* F.O. Pickard-Cambridge (Araneae, Linyphiidae) in Charnwood Forest, Leicestershire, and other new county records. *Ent. Mon. Mag.* **91,** 236-237.

In December 1953, this spider was found at about 600 ft. in Charnwood Forest among relict montane plants. It was hitherto known only from altitudes of 2,000 ft or more, except for a record from the Orkney Islands, where it occurred at not more than 100 ft. Lists of spiders taken at altitudes of 600 and 850 ft in Charnwood, including seven other new records for the county, are also given.

Elliott, R. & Ramakrishna (1956). Insecticide resistence in *Anopheles gambiae* Giles. *Nature, Lond.* **177,** 532-533.

Describes experiments checking susceptibility of this species to DDT and dieldrin. Suggests local differences in this enables species to survive present control methods.

Goodbody, I. M. (1955). Field notes on the corn bunting (*Emberiza calandra*); habitat and distribution in Aberdeenshire. *Scot. Nat.* **67,** 90-97.

The bird is closely associated with farmland at a fairly low altitude, and appears to be dependent on the availability of corn as food at certain periods of the year.

Goto, H. E. (1956). *Folsomia cavicola* Delamare Debouteville, 1954 (Collembola, Isotomidae) new to Britain and a record of fungi parasitic on Collembolan eggs. *Ent. Mon. Mag.* **92,** 12-13.

F. cavicola is recorded from sheep's dung 6 ins. below the soil surface in Anglesey. Eggs hatched in about 17 days at 17° C., and during the first 12 days were liable to infection by the fungus, *Fusarium moniliforme* var. *subglutinans*, which prevented development; some were also infected by *Cephalosporium muscarium*, which is also recorded from eggs of *Tomocerus longicornis*. A species of *Penicillium* on eggs of *T. minor* may not have been pathogenic.

Haddow, A. J. (1956). Rhythmic biting activity of certain East African mosquitoes. *Nature, Lond.* **177,** 531-532.

Forest mosquitoes show a bimodal activity with peaks in the late evening and before sunrise. A comparison between *Taeniorhynchus* and caddis *Cheumatopsyche*.

Hale, W. G. (1955). Overland movement of redshank family. *Brit. Birds*, **48,** 455.

Chicks were moved a mile to a water-hole by the third day after hatching. It is stated that carrying of chicks over obstacles in order to bring them to water is not unusual.

Harley, J. L. (1956). The mycorrhiza of forest trees. *Endeavour*, **15,** 43-48.

Experimental evidence indicates that in the case of forest trees root-fungal associations act as highly efficient aerobic accumulators of ions, assisting both plant and fungi in competition for nutrients with other organisms in the soil.

Harper, P. S. (1955). A comparison of the catches in moth traps placed at ground level and at 80 feet above the ground. *Mag. Blundell's Sch. Sci. Soc.* **10,** 11-20.

Detailed records of moths taken by two mercury-vapour light traps run, one at ground level the other on a tower 80 feet high, between May and July 1955, with an analysis of the comparative catches. Analysis of totals of different species reveal that they may fly at different levels.

Hayhurst, H. (1953). Entomological problems in warehouses. *J. Soc. Brit. Ent.* **4,** 140-144.

Hinton, H. E. (1953). Some adaptations of insects to environments that are alternately dry and flooded, with some notes on the habits of the Stratiomyidae. *Trans. Soc. Brit. Ent.* **11** (10), 209-227.

A review in which species are classified into those that can tolerate complete dehydration and have permeable cuticles, those with impermeable cuticles and spiracular gills, a plastron, or relatively permeable cuticular areas that can be covered by impermeable areas. The hydrostatic and respiratory functions of the air bubble held by a caudal fringe of setae in *Oxycera* larvae are discussed.

Hinton, H. E. (1955). Protective devices of endopterygote pupae. *Trans. Soc. Brit. Ent.* **12** (2), 49-92.

A general account not restricted to British species, in which both passive protective devices including spines, defensive fluids and special protective resemblances; and non-passive devices such as pupal mandibles, gin-traps, spines and poison reservoirs are classified and discussed. A distinction is drawn between large predators, chiefly vertebrates, and small invertebrate predators. Protection against these two classes is frequently afforded by quite different characters: thus ladybird pupae have gin-traps which protect them from mites and an aposematic colour pattern and distastefulness against vertebrates.

Howe, R. W. (1955). Studies on beetles of the family Ptinidae. 12. The biology of *Tipnus unicolor* Pill. and Mitt. *Ent. Mon. Mag.* **91,** 253-257.

An account of laboratory studies on the development cycle and oviposition under controlled conditions, with a comparison of the findings with those for other Ptinids.

Hudson, V. R. Dyson- & Vockeroth, J. R. (1955). Some natural habitats of larvae of *Drosophila subobscura* Collin and *D. macularis* Villeneuve (Dipt., Drosophilidae). *Ent. Mon. Mag.* **91,** 247-248.

Adults of both species were reared from stems of *Typha latifolia*, of which the most heavily infested contained 21 nymphs of *macularis* and 18 of *subobscura*, in Oxon. Adults of *D. subobscura* were also reared from the pedicel of *Rumex* mined by larvae of the cordilurid fly, *Norellisoma spinimanum*. *D. macularis* is uncommon and was not represented in extensive fruit-bait collections; it did, however, visit fermenting fruit placed among *Typha*.

Hughes, R. E. (1956). The purpose of a Nature Reserve. *Nature in Wales,* **2** (1), 213-219.

A brief account of the function of a Nature Reserve is followed by a list and descriptions of the four so far established in Wales.

Hurrell, H. G. (1956). A raven roost in Devon. *Brit. Birds,* **49,** 28-31.

The establishment of a roost of ravens coincided with sheep being killed by snow-drifts and rabbits by myxomatosis. It is suggested that gregarious feeding and roosting of non-breeders may save them from exclusion from the territories of breeding pairs.

Kalmus, H., Satchell, J. E. & Bowen, J. C. (1955). On the colour forms of *Allolobophora chlorotica* Sav. (Lumbricidae). *Ann. Mag. Nat. Hist.* (12) **8,** 795-800.

This earthworm occurs in two forms, a pink and a green. Woodland populations are all pink, those of permanent grassland are often all green. The difference is probably due to a single gene; pink may be the dominant. Neither of the two forms is affected by ultra-violet light.

Kettlewell, H. B. D. (1955). How industrialization can alter species. *Discovery,* **16,** 507-511.

Correlation of the increasing incidence of dark mutants ('industrial melanics') in macrolepidoptera with the degree of air pollution. Black specimens of *Biston betularia* form at least 50% of the populations of that species on the east coast of England, and probably give a true measurement of the pollution. Differences in physiology and habit are noted.

Lack, D. (1956). Seaward flights of swifts at dusk. *Bird Study,* **3,** 37-42.

Records preliminary observations of swifts setting out to sea in summer dusk off the east coast, either after feeding over a mere or at the end of a coasting weather movement. Suggests that the birds were strangers to the district and that they stayed overnight at sea. Proposes a B.T.O. inquiry.

Leatherdale, D. (1956). Fungi associated with gall-forming Trypetidae (Dipt.). *Ent. Mon. Mag.* **92,** 22.

Dead larvae of *Urophora jaceana* in galls on *Centaurea nigra* in Berks. were infected with a fungus tentatively determined as *Aegerita insectorum*; when several were present in one flower bud, all were infected. *Puccinia suaveolens* commonly infected *Cirsium arvense* in Surrey, but the uredosori were most numerous on galls of *U. cardui* where these were present.

Long, D. B. (1955). Observations on sub-social behaviour in two species of Lepidopterous larvae, *Pieris brassicae* L. and *Plusia gamma* L. *Trans. R. Ent. Soc. Lond.* **106,** 421-437.

The formation and maintenance of the aggregations of *P. brassicae* larvae was assisted by the guiding effect of the silken trails spun by the larvae. Contact between the larvae of *P. gamma* was assisted by the restrictive effect of their preference in the age of the food leaves and by a strong phototropism. Larval contact was responsible for setting up, in *P. brassicae*, a mass feeding rhythm; in *P. gamma* it was responsible for aggregation, the production of darker larvae and the reduction of larval duration. The mass feeding rhythms of *P. brassicae* and repeated larval contact in *P. gamma* induced a higher level of activity.

McMahon, E. (1954). Investigations on the hatching of the eggs of the lemon wheat blossom midge (*Contarinia tritici*). *Sci. Proc. R. Dublin Soc.* (N.S.) **26,** 339-345.

This midge (*Contarinia tritici*) caused extensive damage to crops in southern Ireland in 1951, 1952 and 1953. A preliminary study of the effects of temperature and humidity on hatching of the eggs showed that an increase in temperature shortened the hatching time and also the time of production of the wheat anthers. A decrease in humidity prolonged hatching until after the blossoms had opened, so that eggs laid on the margins of the pales were killed by desiccation.

Marshal, A. J. & Disney, H. J. de S. (1956). Photostimulation of an equatorial bird (*Quelea quelea*, Linnaeus). *Nature, Lond.* **177,** 143-144.

Experiments conducted show that male birds near the end of post nuptial testis metamorphosis are susceptible to photostimulation of 17 hours daily, which they never experience naturally. No effect on females. There is no support for Wolfson's summation theory — birds subjected to an extra 5 minutes per day illumination (normal is 10 minutes) totalling 275 minutes over the experimental period, showed no significant difference in gonad structure. Environmental conditions following rain together with the internal rhythm may determine breeding onset.

Matheson, C. (1956). Fluctuations in partridge populations. *Brit. Birds*, **49,** 112-114.

Comparison of records in a Norfolk and in a Cardiganshire game-book seem to show a correlation between the peak periods in the two localities.

Mayr, E. (1956). The interpretation of variation among the yellow wagtails. *Brit. Birds*, **49,** 115-119.

The importance of field observations in solving the relationships of this group is stressed. The large number of forms is attributed to compression in relic areas of widely separated populations at an unknown time.

Moore, B. R., Woodroffe, G. E. & Sanderson, A. R. (1956). Polymorphism and parthenogenesis in a ptinid beetle. *Nature, Lond.* **177,** 847-848.

Ptinus latro and *P. hirtellus* males are morphologically identical whilst the females are distinct. *P. latro* female shown to be peculiarly parthenogenetic. The virgins give no offspring, but mating with *P. hirtellus* males gives rise to an all female progeny, suggesting that the two forms are a polymorphic species. Sterile *latrus* males mated with *latrus* females led to non-viable eggs. Sperm plays a part in the activation of the egg.

Page, F. J. Taylor (1955). Notes on roe deer. *Oryx*, **3,** 157-158.

A brief account of habits, and the formation of roe deer rings.

Panting, P. (1955). Observations of adders in north Pembrokeshire. *Nature in Wales*, **1** (4), 172-174.

Conditions in north Pembrokeshire are not suitable for the grass snake but appear very favourable for the adder, which is abundant. An account is given of the habits of the adder and of local colour variations.

Riney, T. (1956). Differences in proportion of fawns to hinds in red deer (*Cervus elephas*) from several New Zealand environments. *Nature, Lond.* **177,** 488-489.

Five localities are compared, and within successive years. Highly significant differences in hind/fawn ratio. Not unexpected as deer range over a wide variety of habitats and as stags have differing amounts of fat reserves.

Side, K. C. (1955). A study of the insects living on the wayfaring tree. *Leafl. Amat. Ent. Soc.* **27,** 1-20. (1*s.* 7½*d.* post free, from 1 West Ham Lane, London, E.15).

A study of the food chains associated with the wayfaring tree, *Viburnum lantana*, during 1952 and 1953. The summary fauna list appended includes also some spiders, mites, woodlice and snails.

Southwood, T. R. E. & Scudder, G. G. E. (1956). The bionomics and immature stages of the thistle lace bugs (*Tingis ampliata* H.-S. and *T. cardui* L.; (Hem., Tingidae). *Trans. Soc. Brit. Ent.* **12** (3), 93-112.

Describes life histories and food plants of these two plant bugs with full details of all stages and illustrations of eggs and larvae and key to larvae. Notes on a mymarid parasite (*Anaphes*) in eggs of *T. ampliata*. Discusses distribution on host plants and geographically.

Steel, W. O. (1955). Notes on the habitats of some British *Bledius* species (Col., Staphylinidae). *Ent. Mon. Mag.* **91,** 240.

The maritime species, *B. spectabilis*, *B. germanicus* and *B. tricornis* occur in distinct habitats with no overlapping, but *B. unicornis* has been found in the same habitats as the first two and is also recorded in the literature from inland localities. Of the first three species, *B. spectabilis* is the rarest and occurs in sand below high-tide mark on various types of shore; *B. germanicus* is the commonest and occurs in salt marshes and in sand, mud and clay near the sea, where the surface is always moist, but infrequently covered with water; and *B. tricornis* occurs in salt marshes or similar situations where the surface periodically dries up to a depth of about an inch and becomes hard.

Swaine, C. M. (1955). Starlings disabling swifts. *Brit. Birds,* **48,** 552.

Two instances of a swift being disabled by starlings. Editorial comment shows that either species may be killed when competing for nest sites.

Thomas, D. C. (1956). Notes on the biology of some Hemiptera Heteroptera. V. Piesmatidae, Reduviidae and Tingidae. *Entomologist,* **89,** 13-15.

Notes on various aspects of the bionomics of *Piesma quadratus*, *Empicoris culiciformis*, *Derephysia foliacea* and *Lasiacantha capucina*.

Thompson, J. L. Cloudsley- (1955). The life-histories of the British cribellate spiders of the genus *Ciniflo* Bl. (Dictynidae). *Ann. Mag. Nat. Hist.* (12) **8,** 787-794.

Habitats, geographical distribution, relations between individuals, number of eggs, life cycle.

Thornton, I. W. B. (1954). The British species of *Elipsocus* Hagen (Corrodentia, Mesopsocidae). *J. Soc. Brit. Ent.* **5,** 47-64.

Discusses geographic distribution and mating behaviour.

Tutt, H. R. (1956). Nest-sanitation and fledging of the green woodpecker. *Brit. Birds,* **49,** 32-36.

Swallowing or removal of excreta ceases a few days before the young are fledged, causing an accumulation in the nest-hole. In summer roosting in the open, squatting along branches, is probably usual.

Wallace, H. R. (1956). Migration of nematodes. *Nature, Lond.* **177,** 287-288.

Describes an apparatus for determining optimum hydrostatic pressure deficiency for eel worm migration. Experiments show a relationship between water distribution in sand and migration, in *Ditylenchus dipsaci* and *Heteroda schachtii*.

Yapp, W. B. (1955). The birds of Welsh high level oakwoods. *Nature in Wales,* **1,** (4), 161-166.

A comparison between the oakwood groups of Carmarthen, Cardigan and Brecon, with the lowland sessile oakwood of Wyre Forest in Worcestershire; and of the oakwoods to the south of Snowdon with the comparable Lake District woods. The flora in the different woods is compared, and a list given of birds recorded in 416 minutes moving-time in 11 west Welsh oakwoods.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Armsen, P. (1955). Tables for significance tests of 2×2 contingency tables. *Biometrika,* **42,** 494-511.

Five per cent and one per cent levels for one-tail and two-tail tests on contingency tables in which the total number of observations does not exceed fifty.

Bagenal, M. (1955). A note on the relations of certain parameters following a logarithmic transformation. *J. Mar. Biol. Ass. U.K.* **34,** 289-296.

Application to plankton catches considered.

Barnes, H. (1955). Climatological and salinity data for Millport, Scotland. *Glasgow Nat.* **17,** 193-204.

Data on temperature, rainfall, surface salinity, wind speed and direction at this well-known marine biological station.

Bowden, K. F. (1955). Physical oceanography of the Irish sea. *Fish. Invest. Lond.* (2) **18** (8), 1-67.

An analysis, amply charted, of temperature, salinity, tidal and non-tidal currents and of the processes affecting them throughout the Irish Sea area.

Chapman, D. G. (1955). Population estimation based on change of composition caused by a selective removal. *Biometrika,* **42,** 279-290.

The animals removed may be selected for sex, age-class or even species. This method is less efficient than capture-recapture sampling, but is less liable to bias and may be cheaper. Population estimates and their large sample variances are given for a variety of cases, including a combination of selective removal and capture-recapture.

Corbet, P. S. (1955). The larval stages of *Coenagrion mercuriale* (Charp.) (Odonata: Coenagriidae). *Proc. R. Ent. Soc. Lond.* (A) **30,** 115-126.

Identification of the larvae from the fifth instar onwards.

Cushing, D. H. & Richardson, I. D. (1955). A triple frequency echo-sounder. *Fish. Invest. Lond.* (2) **20** (1), 1-18.

Describes an echo sounder comprising three oscillators of 10, 14 and 30 kilocycles mounted alongside each other. This was tested, in good weather only, on shoals of cod, herring and unidentified traces, and the results analysed statistically. Comparison with earlier work shows great differences in frequency ratios for different sizes, and possibly species of fish, and suggests that the apparatus may be of use in physical identification of shoals.

Cushing, D. H. & Richardson, I. D. (1956). A record of plankton on the echo-sounder. *J. Mar. Biol. Ass. U.K.* **35,** 231-240.

The characteristics of the echo trace produced by plankton organisms is described.

Eastop, V. F. (1955). Selection of aphid species by different kinds of insect traps. *Nature, Lond.* **176,** 936.

Moereke yellow traps are checked against a suction trap. Some species (largely feeders on dicotyledons) are selected 30 times as strongly as others (feeding on grass and sedge) by yellow traps. Also more sunshine increases the yellow trap to suction trap ratio.

Evans, G. O. & Browning, E. (1955). Techniques for the preparation of mites for study. *Ann. Mag. Nat. Hist.* (12) **8,** 631-635.

The methods do not apply to fresh-water or marine species.

Gurr, L. (1955). A pneumatic nest-recording device. *Ibis,* **97,** 584-586.

A device, consisting of two tambours connected by a rubber tube and a clockwork kymograph drum, records movements of the sitting bird as well as on and off movements.

Hannan, E. J. (1955). An exact test for correlation between time series. *Biometrika,* **42,** 316-326.

Gives new estimates of the significance of the correlations between the populations of game birds discussed by P. A. P. Moran (1952, *J. Anim. Ecol.* **21,** 154-158).

Hill, A. R. (1955). A bivalve cage for small Arthropods. *Proc. R. Ent. Soc. Lond.* (A) **30,** 167-168.
Describes a cage suitable for use in studying small leaf-eating arthopods *in situ.*

Hincks, W. D. (1952). The British species of the genus *Ooctonus* Haliday, with a note on some recent work on the fairy flies (Hym., Mymaridae). *Trans. Soc. Brit. Ent.* **11** (7), 153-163.
Keys to and description of the British species with recorded distribution by vice-counties.

Holme, N. A. (1955). An improved 'vacuum' grab for sampling the sea-floor. *J. Mar. Biol. Ass. U.K.* **34,** 545-551.
An instrument which makes use of hydrostatic pressure to obtain a small unstratified sample of the sea-floor is described.

Hynes, H. B. N. (1955). The nymphs of the British species of *Capnia* (Plecoptera). *Proc. R. Ent. Soc. Lond.* (A) **30,** 91-96.
With a key to the nymphs of the British species of *Capnia.*

Joyce, R. J. V. (1956). Insect mobility and design of field experiments. *Nature, Lond.* **177,** 282.
Immigration of insects from control plots to sprayed plots increases the crop yield of the control plots. Jassid counts in cotton fields show this movement. *Empoasca* may move into the sprayed regions and die. On the other hand the immature stages of the cotton white fly in Sudan are immobile and the predators are mobile, hence the fly increases in unsprayed plots.

Kevan, D. K. (1955). The identification of *Badister peltatus* (Pz.), *dilatatus* Chaud. and *anomalus* (Perris) (Col., Carabidae, Licinini). *Ent. Mon. Mag.* **91,** 207-210.
Includes a key to the adults of these three British species, with their distribution in Britain.

Pitcher, R. S. (1955). The larval instars of some gall midges of the genus *Thomasiniana* Strand, E., 1916 (Diptera: Cecidomyidae). *Proc. R. Ent. Soc. Lond.* (A) **30,** 97-102.
An account, which enables the instars to be separated, is given of each of the three larval instars of *Thomasiniana theobaldi, T. oculiperda, T. fructicosi* and *T. crataegi.*

Pringle, J. W. S. (1956). Insect song. *Endeavour,* **15,** 68-72.
Variations in insect song, inaudible to the human ear, can now be studied with modern recording devices. Methods of sound production are considered, and characteristic sounds for insect species are shown to be caused by differences in the time distribution of sound pulses rather than by differences in pitch or tone quality.

Sayer, H. J. (1956). A photographic method for the study of insect migration. *Nature. Lond.* **177,** 226.
By using double exposure at short intervals of time, the orientation and speed of migrating locusts can be determined.

Waugh, W. A. O'N. (1955). An age-dependent birth and death process. *Biometrika,* **42,** 291-306.
A stochastic process in which each individual eventually either dies or divides into two. The probability of extinction, and the mean, the variance and the coefficient of variation of the population size are given for various relations of the birth rate to the death rate.

Woodroffe, G. E. (1956). *Macrolophus costalis* Fieber (Hem Miridae), a hitherto unrecognized British species. *Entomologist,* **89, 37-38.**
This Mirid, from bramble (*Rubus* agg.), has hitherto been confused with *M. nubilis* on *Stachys,* and a key for their separation is included.

Yarrow, I. H. H. (1954). The British ants allied to *Formica fusca* L. (Hym. Formicidae). *Trans. Soc. Brit. Ent.* **11** (11), 229-244.
Includes keys, notes on distribution, etc.

3. PARASITES

Allen, P. (1955). Parasites from *Depressaria heracliana* (L.) (Lep., Oecophoridae). *Ent. Mon. Mag.* **91,** 198.

16 females and 78 males of *Litomastix serricornis* and 24 females and one male of *Tyndarichus scaurus* (a possible hyperparasite) were reared from a larva of *D. heracliana*. Some species of *Litomastix* are polyembryonic, and the presence of both sexes is possibly due to the deposition of two eggs in the host larva.

Arthur, D. R. (1955). The larva of *Ixodes rothschildi* Nuttall & Warburton, 1911. *Ann. Mag. Nat. Hist.* (12) **8,** 711-712.

Description of this tick larva. From a Lundy puffin.

Dunnet, G. M. & Allan, R. M. (1955). Annual and regional variations in the flea populations of nests of the house-martin *Martula u. urbica* (L.) in north-east Scotland. *Ent. Mon. Mag.* **91,** 161-167.

During several years' survey of unoccupied house-martin's nests in inland and sea-cliff colonies 7 fleas were found, of which *Frontopsylla laeta*, *Orneacus waterstoni* and *Dasypsyllus gallinulae* (recorded from this host for the first time) were confined to coastal colonies. The inland nests were all on buildings, and the fleas found in them also occurred in the cliff nests. The flea fauna varied among the coastal and among the inland colonies. The data include extensions of range for *Ceratophyllus rusticus* and *C. farreni*. Nests in an inland quarry contained *C. hirundinis*.

Emerson, K. C. (1955). A new mallophaga from a loon. *Ann. Mag. Nat. Hist.* (12) **8,** 718-720.

Reduces the number of species from loons or divers (*Gavia* or *Colymbus*) to two. *Craspedonirmus colymbinus* from *G. arctica* and *G. stellata* (black- & red-throated divers), and *C. immer* from *G. immer* (the great northern diver).

Healy, A. (1956). A parasite of salmon. *Irish Nat. J.* **12,** 41.

The cestode *Hepatoxylon trichiuri* in a salmon.

Hepper, B. T. (1955). Environmental factors governing the infection of mussels, *Mylilus edulis*, by *Mytilicola intestinalis*. *Fish. Invest. Lond.* (2) **20** (3), 1-21.

Field surveys of the rate of infestation of mussels with *Mytilicola* under different ecological conditions in Poole Harbour, Milford Haven and the estuaries of the Tamar, Lynher, Truro and Fowey rivers, supplemented by field experiments at Poole and Fowey with mussels settled on rafts. Mussels raised above the sea-bed or in fast-moving water at either end of an estuary are less infected than those on the bottom or in slow-moving water from the middle of estuaries. Culture methods are proposed to restrict the level of infestation in mussels.

Holland, G. P. (1955). Primary and secondary sexual characteristics of some Ceratophyllinae, with notes on the mechanism of copulation (Siphonaptera). *Trans. R. Ent. Soc. Lond.* **107,** 233-248.

Based on slide preparations of some Ceratophyllinae *in cop.*: *Ceratophyllus idius*, *C. niger*, *C. farreni*, *C. rossittensis swansoni*, *Monopsyllus wagneri* and *Diamanus montanus*.

Jackson, D. J. (1956). Notes on hymenopterous parasitoids bred from eggs of Dytiscidae in Fife. *J. Soc. Brit. Ent.* **5,** 144-149.

Caraphractus cinctus from *Dytiscus marginalis* and *Agabus* and *Ilybius* spp., often in large numbers; *Patasson* sp. from egg probably of *Ilybius fuliginosus* and another unidentified mymarid from the same species; *Prestwichia aquatica* from *I. fuliginosus*; *Chrysocharis* sp. from *Dytiscus marginalis*. Some notes on biology.

Legowski, T. J. (1955). *Triaspis* (*Sigalphus*) *floricola* Wesm. (Hym., Braconidae) parasitising the larvae of clover seed weevils (*Apion* spp.) in E. Anglia. *Ent. Mon. Mag.* **91,** 273-274.

Parasitism of *Apion* sp. or spp. in fields in Cambridgeshire, Hampshire and Essex varied from 20 to 60% in 1954. A maximum of 4 cocoons were obtained from a single flower head.

Rothschild, M. (**1955**). The distribution of *Ceratophyllus borealis* Rothschild, 1906 and *C. garei* Rothschild, 1902, with records of specimens intermediate between the two. *Trans. R. Ent. Soc. Lond.* **107,** 295-317.

The records for the two species and their intermediates are brought together. A tentative taxonomic description of the intermediates is given. Includes a discussion of the way in which the observed distribution may have been brought about.

Shaw, S. (**1956**). *Telenomus punctatissimus* (Ratzeburg) (Hymen, Scelionidae) new to Britain. *J. Soc. Brit. Ent.* **5,** 165-166.

Parasitising eggs of Buff-tip moth (*Phalera bucephala*) in Cheshire. Notes definitive characters of the species.

Smit, F. G. A. M. (**1955**). Two new subspecies of fleas (Siphonaptera) from the British Isles. With a discussion on their distribution by M. Rothschild and F. G. A. M. Smit. *Trans. R. Ent. Soc. Lond.* **107,** 341-372.

A study of *Ceratophyllus styx* and *Ctenophthalmus nobilis* in Britain reveals two new subspecies : *C. styx jordani* and *C. nobilis vulgaris*. Included is a discussion of the distribution of all the subspecies.

Thompson, G. B. (**1955**). Contributions towards a study of the ectoparasites of British birds and mammals. No. 5. *Ann. Mag. Nat. Hist.* (12) **8,** 724-730.

Two species of Diptera Hippoboscidae —the rare *Lynchia albipennis* from ardeid birds and the sheep ked *Melophagus ovinus*.

Thompson, G. B. (**1955**). Contributions towards a study of the ectoparasites of British birds and mammals. No. 6. *Ann. Mag. Nat. Hist.* (12) **8,** 917-927.

United bibliography of the previous five papers, giving all references to the British Diptera Hippoboscidae.

4. FOOD AND FOOD HABITS

Ballantine, D. & Morton, J. E. (**1956**). Filtering, feeding and digestion in the lamellibranch *Lasaea rubra*. *J. Mar. Biol. Ass. U.K.* **35,** 241-274.

Absorptiometric determinations of filtering rates with cultures of *Phaeodactylum tricornutum* were carried out over 3 h periods, and the rates of filtration of various unialgal and mixed cultures were determined. Preliminary digestion, with the reduction of the cell to a 'ghost', takes place extra-cellularly.

Campbell, R. N. (**1955**). Food and feeding habits of brown trout, perch and other fish in Loch Tummel. *Scot. Nat.* **55,** 23-28.

Includes some notes on pike and eels.

Cobnut, G. (**1955**). Foxes and myxomatosis in Kent. *Oryx,* **3,** 156-157.

The majority of foxes appeared from stomach examinations to have gone over to an omnivorous diet. There is no sign of deterioration in health.

Downes, J. A. (**1955**). The food habits and description of *Atrichopogon pollinivorus* sp. n. (Diptera: Ceratopogonidae). *Trans. R. Ent. Soc. Lond.* **106,** 439-453.

Feeding habits are described in detail; briefly, both sexes feed on the nectar of honeysuckle and the females also pierce the pollen grains and ingest the sap.

Dunnet, G. M. (**1955**). The breeding of the starling *Sturnus vulgaris* in relation to its food supply. *Ibis,* **97,** 619-662.

A detailed study of a starling population in a square mile. Leatherjackets are the principal food (80%) of the nestlings. Synchrony of first clutches may be due to the advantage of successful second broods, the occurrence of which is determined by how early breeding starts, and when leatherjackets disappear from the soil. It also provides opportunities for gregarious feeding by adults and juveniles which may have survival value.

Hancock, D. A. (**1955**). The feeding behaviour of starfish on Essex oyster beds. *J. Mar. Biol. Ass. U.K.* **34,** 313-331.

Laboratory and field observations, mainly on *Asterias rubens*. The greater part of the starfish's food is made up of organisms which are competitors of the oyster; it is therefore not such a serious enemy of the oyster as was previously supposed.

Laurence, B. R. (1955). The Empididae (Diptera) of a Yorkshire stream. *Ent. Mon. Mag.* **91,** 220-224.

Observations on the occurrence and on the hunting and mating habits of some 18 Empids along two ½-mile stretches of a stream, with lists of the prey taken by 11 of them and a diagram showing the predator-prey relationships.

Lockie, J. D. (1955). The breeding and feeding of jackdaws and rooks, with notes on carrion crows and other Corvidae. *Ibis*, **97,** 341-369.

Late clutches in the rook are significantly lower than early ones, but not in the jackdaw. Asynchronous hatching in both species is an adaptation to a variable food supply, the smaller young dying when food is short. Rooks obtain food principally by probing on grassland, and nest early so that the young are being fed in April when earthworms are most available, but jackdaws, which feed on the surface, have young later when surface invertebrates are most plentiful.

Moore, B. P. (1955). Notes on carrion Coleoptera in the Oxford district. *Ent. Mon. Mag.* **91,** 292-295.

Includes a table showing the species found at baits (dead squirrels, birds, hedgehog and cat) hung or placed on the ground in deciduous woodland, water meadows, and open sandy country with adjacent mixed woodland, indicating their frequency, date of capture, and the state of decay of the host; a second table showing the species captured on the cat between 30 April and 5 July; and a brief discussion of the results.

Naylor, E. (1955). The diet and feeding mechanism of *Idotea*. *J. Mar. Biol. Ass. U.K.* **34,** 347-355.

This isopod crustacean is potentially an omnivorous scavenger, but each species may have a characteristic diet depending on the availability of food in its particular habitat. The structure and function of organs used in feeding are described.

Owen, D. F. (1954). The swift *Apus apus* L. as a predator of aphids. *J. Soc. Brit. Ent.* **5,** 82-85.

Most of the aphids caught by swifts were of the larger species.

Owen, D. F. (1955). Coleoptera taken by swifts (*Apus apus* L.). *J. Soc. Brit. Ent.* **5,** 105-109.

Comparison with trapping records shows the scarcity of Lathridiidae in the swifts' meals. Almost all the beetles taken were small.

Owen, D. F. (1955). The food of the heron *Ardea cinerea* in the breeding season. *Ibis*, **97,** 276-295.

The study was made by taking food samples from nestlings in three heronries. The population of prey species was different in different heronries and varied with the season. Many nestlings died of starvation. The average weight of food consumed by a brood is estimated at 230 pounds during the nestling period.

Parmenter, L. (1952). Flies visiting greater stitchwort, *Stellaria holostea* Linn. (Caryophyllaceae). *J. Soc. Brit. Ent.* **4,** 88-89.

Twenty-eight species are recorded.

Parmenter, L. & Owen, D. F. (1954). The swift, *Apus apus* L., as a predator of flies. *J. Soc. Brit. Ent.* **5,** 27-33.

Smaller species were selected, but not very small species. The composition of the meals suggests that the swifts fed over open fields bounded by hedges and ditches, streams or rivers or with cattle ponds.

Parmenter, L. (1955). Diptera and other insect visitors to the flowers of *Ranunculus sardous* Craitz. *J. Soc. Brit. Ent.*, **5,** 131-132.

Lists 123 specimens belonging to 24 species of 9 families taken during two hours on sunny days at Flatford Mill, Essex in July 1951.

Scott, H. (1956). Ants frequenting buds of peony and royal lily. *Ent. Mon. Mag.* **92,** 1-4.

Lasius niger visited buds of garden peonies of the *lactiflora* group at Henley and of *Paeonia officinalis* and *P. tenuifolia* in Sussex, attracted by nectar secreted at the edges of the sepals. They also visited young, green buds of *Lilium regale*, though in smaller numbers, working

along the edges of the perianth segments, where the nectaries were evidently already functioning. The ants did not harm the plants.

Scott, M. E. (1955). Nestling blackbirds eating slow-worms. *Scot. Nat.* **67,** 116.

Shearer, W. M. (1955). Fish remains in the stomach of Atlantic salmon. *Scot. Nat.* **67,** 108-109.

Smith, K. G. V. (1952). Observations on the prey and predacious habits of various Empididae (Diptera). *J. Soc. Brit. Ent.* **4,** 90-93.

Tachydromia albifacies eating a small fly, and *Hilara intermedia* taken *in cop.* with Chironomidae and Cecidomyids as prey. *H. quadrivittata* with a psyllid as prey and two pairs *in cop.* with an alate aphid and a male *H. manicata* as prey.

Twinn, D. C. (1955). Notes on the pabulum and biology of *Strangalia quadrifasciata* (L.) (Col., Cerambycidae). *Ent. Mon. Mag.* **91,** 219.

In 1951, larvae were numerous in dry birch stumps 9-12 ins. in diameter in Cheshire, but the stumps were destroyed, and in subsequent years the larvae occurred in others not more than 6 ins. in diameter and with wet, fibrous wood. The larval burrows originated in the lower parts of the stumps and extended into the drier parts, and the pupal chambers were situated in upright stems or dry, exposed roots.

Watson, A. (1955). The winter food of six Highland foxes. *Scot. Nat.* **67,** 123-124.

Yonge, C. M. (1956). *Calanus*: the food of the herring. *Discovery,* **17,** 8-10.

An outline of the biology of *Calanus* and their role in marine food-chains, based upon 'The biology of a marine Copepod' by S. M. Marshall and A. P. Orr.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Allan, R. M. (1955). Observations on the fauna of Heisker or Monach Isles, Outer Hebrides. *Scot. Nat.* **67,** 3-8.

Systematic list of birds and mammals seen in four visits of ten days each during 1953-54.

Andrewes, C. H. (1956). *Helocera delecta* Mg. and other uncommon Diptera in the Isle of Wight. *J. Soc. Brit. Ent.* **5,** 164-165.

Records *Helocera delecta* (Tachinidae), *Phaonia fusca* (Muscidae) and several Dolichopodidae on the island.

Ashe, G. H. (1955). *Oxypoda planipennis* Thoms. (Col., Staphylinidae) from Nethy Bridge, Inverness-shire: a species new to Britain. *Ent. Mon. Mag.* **91,** 248.

Baker, C. S. Wood- (1955). Records of European Aphids (Hem.). *Ent. Mon. Mag.* **91,** 147-153.

Includes records in Britain for some 70 species of 40 genera.

Baynes, E. S. A. (1956). Report on migrant insects in Ireland for 1955. *Irish Nat. J.* **12,** 25-28.

Twelve species of Lepidoptera and one dragonfly were reported during the year.

Beirne, B. P. (1955). Zoogeographical significance of distributional changes in British Macrolepidoptera. *Trans. R. Ent. Soc. Lond.* **107,** 117-123.

T. T. Macan 1953 (J. *Anim. Ecol.* **22,** 172-173) criticizes Beirne (1947, *Trans. R. Ent. Soc. Lond.* **98,** 273-372) on the basis that, because the distribution of some species of butterflies have undergone major changes within the past 150 years, these distributions are not a reliable basis for zoogeographical theories on these species. An analysis of the records shows that species undergoing major distributional changes are exceptional among the British species and that they comprise only 3% of the total. Some species show fluctuations and minor distributional changes may be regular occurrences with relatively common and widely distributed species. Beirne's original thesis appears to be substantially correct; that is, the known distributions are a reliable basis for the construction of historical theories.

Benson, R. B. (1955). Records of sawflies (Hym., Symphyta) from Radnorshire in Wales and the Welsh marches of Herefordshire. *Ent. Mon. Mag.* **91,** 226.

A list of 45 species, of which 11 are new to Wales.

Ben-Tuvia, A. (1955). Two indo-pacific fishes, *Dasyatis uarnak* and *Upeneus moluccensis*, in the Eastern Mediterranean. *Nature, Lond.* **176,** 1177-1178.

Several specimens of the former from off Israel. The latter has become common, and has often been wrongly identified as *Mulloidichthys auriflamma*.

Best, F. C. (1956). Butterflies in Wales. *Nature in Wales,* **2** (1), 205-212.

Of the 55 resident British species 39 are known to occur in Wales, three probably do, and six have occasionally been reported though not confirmed. Seven have never been reported from Wales. Nine of the eleven non-wintering migrants have been recorded.

Birkett, N. L. (1955). *Phalonia implicitana* Wocke in North Lancashire. *Ent. Rec.* **67,** 331.

A first record for Lancashire.

Boyd, A. W. (1955). Mammals of Cheshire. *Oryx,* **3,** 151-155.

Notes on bats, insectivores, rodents, carnivores, pinnipedes, ungulates and cetaceans of Cheshire and its estuaries.

Buck, F. D. (1955). A provisional list of the Coleoptera of Epping Forest. *Ent. Mon. Mag.* **91,** 174-192.

Habitats, dates and localities for a very large number of species, based on collections over many years and on the literature.

Campbell, J. L. (1955). *Thalpophila matura* on the Isle of Rum. *Entomologist,* **88,** 237-238.

A first record for Rum.

Collin, J. E. (1952). On the subdivisions of the genus *Pipizella* Rnd., and an additional British species (Diptera, Syrphidae). *J. Soc. Brit. Ent.* **4,** 85-88.

P. maculipennis taken near Colchester, Essex. *P. annulata* may some day be found in Britain.

Collin, J. E. (1952). Some rare Diptera found in Norfolk, including *Nemotelus fraternus* Loew, an addition to the British list. *J. Soc. Brit. Ent.* **4,** 112-113.

Collin, J. E. (1953). *Clusiaria apicalis* Zett. new to Britain. *J. Soc. Brit. Ent.* **4,** 139-140.

Breeding in an old birch log at Kincraig, Inverness-shire.

Collin, J. E. (1953). Some additional British Anthomyiidae (Diptera). *J. Soc. Brit. Ent.* **4,** 169-177.

Lists a number of species, some new to science.

Collin, J. E. (1954). *Tipula siebkei* Zetterstedt (1852), an addition to the British Tipulidae (Diptera). *J. Soc. Brit. Ent.* **5,** 72.

A male was taken in the New Forest, Hants, in June 1953.

Collin, J. E. (1955). Genera and species of Anthomyiidae allied to *Chirosia* (Diptera). *J. Soc. Brit. Ent.* **5,** 94-100.

Includes notes on distribution.

Collin, J. E. (1955). *Syndyas nigripes* Zetterstedt, an Empid genus and species new to the British fauna. *J. Soc. Brit. Ent.* **5,** 132-133.

A number of specimens were swept from the herbage in a bog in the New Forest in July 1954.

Collin, J. E. (1956). Some new British Borboridae (Diptera). *J. Soc. Brit. Ent.* **5,** 172-178.

Records and descriptions of several genera and species of borborid flies.

Connell, J. H. (1955). *Elminius modestus* Darwin, a northward extension of range. *Nature, Lond.* **175,** 954.

Record of this Australian barnacle from the Isle of Cumbrae, Scotland. It had previously been recorded mainly in the south of England, and has been spreading round the coast of Britain.

Cooke, J. A. L. & Lampel, G. P. (1953). *Pirata uliginosus* Thor. (Araneae, Lycosidae) in Shropshire, and some further additions to the county records of spiders. *J. Soc. Brit. Ent.* **4,** 186-187.

Coombs, C. W. & Woodroffe, G. E. (1955). An annotated check list of the British species of *Cryptophagus* (Herbst) (Col., Cryptophagidae). *Ent. Mon. Mag.* **91,** 249-250.

Dance, S. P. (1956). A new Sussex locality for *Pisidium pseudosphaerium* Favre. *J. Conch.* **24,** 91-92.

Account of the habitats of a rare freshwater bivalve in marsh drains near Lewes, with associated Mollusca.

Duffey, E. (1955). Notes on the natural history of Eynhallow, Orkney. *Scot. Nat.* **67,** 40-51.

Mainly birds, but also mammals and invertebrates.

Duffey, E. & Millidge, A. F. (1954). *Centromerus incilium* (L. Koch), a Linyphiid spider taken near Oxford, with notes on related species. *J. Soc. Brit. Ent.* **4,** 218-223.

Dunn, M. H., Hunter, W. R. & Dunn, A. (1954). The birds of the Garvelloch Islands. *Glasgow Nat.* **17,** 142-146.

The breeding birds of a small archipelago in the Firth of Lorne.

Eady, R. D. (1952). A revision of Section 1 (Mayr, 1872) of the genus *Symergus* (Hym. Cynipidae) in Britain, with a species new to science. *Trans. Soc. Brit. Ent.* **11** (6), 141-152.

S. clandestinus from Herts.

Eggeling, W. J. (1955). The breeding birds of the Isle of May. *Scot. Nat.* **67,** 72-89.

Thirty-seven species have been recorded as breeding on this small island in the Firth of Forth.

Evans, L. Lloyd- (1956). *Ena montana* (Draparnaud) in Hertfordshire. *J. Conch.* **24,** 102.

First authentic record of this land snail living in the county, with description of habitat.

Evans, L. Lloyd- (1956). Occurrence of Lake Limpet (*Acroloxus lacustris*) in Llyn Gafr, Merioneth. *Nature in Wales,* **2** (1), 225-226.

This species has not hitherto been recorded from Merionethshire and is rare or absent over much of Wales.

Fraser, J. H. (1955). The salp *Ritteriella* off the English coast—a correction. *J. Mar. Biol. Ass. U.K.* **34,** 247-248.

Note on specimens taken by H.M.S. *Challenger.*

Goto, H. E. (1953). Notes on the Collembola of the British Isles. *J. Soc. Brit. Ent.* **4,** 177-182.

Goto, H. E. (1955). Collembola from Shillay, Outer Hebrides, including new British and local records. *Scot. Nat.* **67,** 29-33.

Goto, H. E. (1955). Some new British and local records of Collembola. *Ent. Mon. Mag.* **91,** 267-268.

53 new county records are given for 24 species, with dates, localities and habitats. They include *Bourletiella flava,* recorded for the first time in Britain from Hampshire.

Hall, R. E. (1952). Some Chironomidae (Diptera) from the Shetland Islands. *J. Soc. Brit. Ent.* **4,** 66-69.

All the species are well known British forms, mostly generally distributed.

Hall, R. E. (1954). Some Chironomidae (Diptera) from southern Hampshire. *J. Soc. Brit. Ent.* **4,** 215-218.

Harding, J. P. & Gervers, F. W. K. (1956). Occurrence of *Actheres percarum* Nordmann in English waters. *Nature, Lond.* **177,** 664-665.

From perch, and may have been introduced from continent.

Hewson, R. (1955). The mountain hare in the Scottish islands. *Scot. Nat.* **67,** 52-60.
Lepus timidus scoticus or *L. t. hibernicus* were introduced on many Scottish islands during the 19th century, and the former survives on many of them.

Hincks, W. D. (1952). A new 'fairy fly' from the Spurn Peninsula (Hym. Mymaridae). *J. Soc. Brit. Ent.* **4,** 64-66.
Lymaenon fossarum, closely related to *L. longicauda.*

Hincks, W. D. (1954). Rare Trypetids (Diptera) at Miller's Dale, Derbyshire. *J. Soc. Brit. Ent.* **5,** 88.
Records *Rhacochlaena toxoneura* (Loew) and *Crytaciura rotundiventris* (Fallén) both new to Derbyshire.

Hincks, W. D. (1956). Notes on three species of micro-Hymenoptera from Charterhouse Pools. *J. Soc. Brit. Ent.* **5,** 150-152.
Records *Lymaenon alecto, Inostemma boscii* and *I. spinulosum* from this Somerset locality.

Hitchings, G. J. (1956). *Platyrrhinus resinosus* Scop. (Col., Anthribidae) in Kent. *Ent. Mon. Mag.* **92,** 15.
A new county record.

Hunter, W. Russell & Hunter, M. Russell (1956). Mollusca on Scottish mountains. *J. Conch.* **24,** 80.
Records of slugs and snails at altitudes of above 2000 ft.

Jackson, D. J. (1955). Further notes on beetles from the island of Raasay and some Scottish records of Donaciinae. *Scot. Nat.* **67,** 34-39.

Kevan, D. K. McE. (1952). A summary of the recorded distribution of British Orthopteroids. *Trans. Soc. Brit. Ent.* **11** (8), 165-180.
Distribution by vice-counties.

Kevan, D. K. McE. (1953). Notes on the distribution of British Orthopteroids. *J. Soc. Brit. Ent.* **4,** 119-122.
Leptophyes punctatissima is the only flightless native British Orthopteroid from the Isle of Man.

Kevan, D. K. McE. (1953). Additional notes on the distribution of British Orthopteroids. *J. Soc. Brit. Ent.* **4,** 183-185.

Kevan, D. K. McE. (1954). Further notes on the distribution of British Orthopteroids. *J. Soc. Brit. Ent.* **5,** 65-71.

Kidd, L. N. (1954). Notes on some Derbyshire craneflies. *J. Soc. Brit. Ent.* **5,** 86-87.

Kidd, L. N. (1954). *Scoliocentra villosa* (Meigen) (Dipt., Helomyzidae) and *Trichocera maculipennis* Meigen (Dipt., Trichoceridae) taken in Derbyshire caves. *J. Soc. Brit. Ent.* **5,** 87-88.

Kidd, L. N. (1955). A new species of *Mycomyia* (Dipt., Mycetophilidae) taken in Cumberland. *Ent. Mon. Mag.* **91,** 258.
Mycomyia britteni taken at Skirwith, 24 August 1953.

Leston, D. (1956). The British species of *Sigara* (*Sigara*) Fabricius (Hem., Corixidae). *J. Soc. Brit. Ent.* **5,** 153-158.
The common British waterbug is not the Continental *Sigara striata* but *S. dorsalis*; *S. striata* however occurs in S.E. England. Detailed characters and drawings are given for separating the two species and their British distribution is discussed.

Lewis, T. (1955). Two interesting British records of Thysanoptera. *J. Soc. Brit. Ent.* **5,** 110-113.
Records *Abiastothrips schaubergeri* (Pries.) new to Britain and *Euchaetothrips kroli* (Schille) new to Nottinghamshire.

Lindroth, C. H. (1955). Insects and spiders from Fair Isle. *Ent. Mon. Mag.* **91,** 216.

14 species, comprising one each in Thysanura, Dermaptera, Hemiptera and Hymenoptera, 8 Coleoptera, and 2 Arachnids, were collected on Fair Isle in October 1952. Only two of them fly regularly and two or three may be able to rise more or less accidentally into the air.

Lindroth, C. H. (1956). Some Coleoptera from south-western England. *Ent. Mon. Mag.* **92,** 9-10.

A list of beetles from habitats such as wharves, quays, railway embankments and the neighbouring sea-shore at former ballast-places in Devon, Dorset and Cornwall, from which sailing vessels formerly left for Canada. It includes many species not given in previous local lists of other authors.

Massee, A. M. (1954). The Hemiptera-Heteroptera of Kent. *Trans. Soc. Brit. Ent.* **11** (12), 245-280.

Includes notes on distribution, habitat, host plants, hibernation, etc.

Massee, A. M. (1955). *Strongylocoris leucocephalus* (L.) (Hem., Miridae) found in Kent. *Ent. Mon. Mag.* **91,** 268.

A new county record. The Mirids were associated with *Galium verum*, but were not observed to feed on it.

Massee, A. M. (1955). *Trapezonotus dispar* Stål (Hem., Lygaeidae) noted in Suffolk. *Ent. Mon. Mag.* **91,** 274.

A new county record.

Massee, A. M. (1955). *Longitarsus quadriguttatus* Pont. (Col., Chrysomelidae) found in Kent. *Ent. Mon. Mag.* **91,** 285.

A new county record.

Moez, M. K. Abdel- & Humphries, C. F. (1955). A description of a new nereid—*Nereis southerni*. *Proc. R. Irish Acad.* **57** (B), 147-153.

Occurs subtidally in shallow water in fine muddy sand and in clay, at densities of up to 300 per square metre, in Ireland and Denmark.

Moreau, R. E. (1956). The Iberian peninsula and migration. *Bird Study*, **3,** 1-25.

Discusses the migration of birds through and into Portugal and Spain, on the evidence of collated ringing recoveries (listed in detail), of the regular appearance there, on passage or in winter, of birds which breed elsewhere in Europe, and of records of visible migration, mostly over the Pyrénées and the east and north coasts. Many European passage migrants reach the extreme west of the peninsula and must change direction on leaving, in order to winter in the Sahara.

Muir, D. A. (1954). A note on insects from the Garvelloch Islands. *Glasgow Nat.* **17,** 140-141.

Lepidoptera, Formicidae and Diptera collected on a small archipelago in the Firth of Lorne.

Odell, N. E. (1956). So-called 'glacier-worms' in New Zealand. *Nature, Lond.* **177,** 534.

Identified as chironomids.

Parmenter, L. (1952). *Coenia curvicauda* Mg. (Diptera, Ephydridae) an overlooked species. *J. Soc. Brit. Ent.* **4,** 89-90.

Taken on plants growing in mud at Bookham Common, Surrey in April, 1951.

Parmenter, L. (1953). *Agathomyia falleni* Zett. (Dipt., Platypezidae); an addition to the British list. *J. Soc. Brit. Ent.* **4,** 122-123.

Taken at Box Hill, Surrey, in September, 1952.

Payne, R. M. (1955). *Stenobothrus lineatus* Panz. in Hertfordshire. *Ent. Rec.* **67,** 241-245.

A colony found in south-east Herts. on 31 July 1955 constitutes the second record for this county. It comprised only males, and occurred in dry grassland at an altitude of 180 ft where the chalk was near the surface. *Omocestus viridulus* and *Chorthippus parallelus* were plentiful.

Payne, R. M. (1955). *Decticus verrucivorus* (L.) (Orth., Tettigoniidae) in Sussex. *Ent. Mon. Mag.* **91,** 263.

A new county record.

Pearce, E. J. (1956). An additional record for *Neuraphes planifrons* Blatch (Col., Scydmaenidae). *Ent. Mon. Mag.* **92,** 19.

N. planifrons is recorded, for the first time in the midlands west of the Severn, from Monmouth, where it attacked alder. This is the first record from this food plant.

Ragge, D. R. (1955). Rediscovery of *Decticus verrucivorus* (L.) in Dorset (Orth. Tettigoniidae). *Entomologist,* **88,** 260-261.

This grasshopper not recorded in the British Isles for 28 years, was found in August 1955 in north-western Purbeck among ling bordering a small pond on a very dry, sandy heath. *Chorthippus vagans* was abundant in the same area and is evidently distributed over the whole of north-western Purbeck (see 1954 *Entomologist,* **87,** 230-231 and abstract in 1955 *J. Anim. Ecol.* **24,** 493.)

Richardson, A. (1956). *Eurois occulta* in Yorks. and Glos. *Entomologist,* **89,** 47.

A new record for Gloucestershire.

Roberts, B. & Atkinson, R. (1955). The Haskeir Rocks, North Uist. *Scot. Nat.* **67,** 9-18.

Observations on seals (*Halichoerus grypus*) and birds on two short visits in June 1952 and July 1953.

Roy, A. B. (1955). The spiders of the Black Wood of Rannoch. *Scot. Nat.* **67,** 19-22.

A list with few details of habitat.

Russell, H. M. (1955). A note on some Yorkshire Diptera. *Ent. Mon. Mag.* **91,** 239.

The seven species of various families that are listed include *Anthracophaga strigula,* which is new to Yorkshire; there are also several new vice-comital records.

Ruttledge, R. F. (1956). An ornithological visit to Inishmurray. *Irish Nat. J.* **12,** 28-29.

A list of the birds seen on 13 July 1955, on Inishmurray, a hitherto ornithologically unvisited island off the coast of Co. Sligo.

Sage, B. L. (1955). Notes on some Arachnida recorded in Wales in 1954. *Nature in Wales,* **1** (4), 174-176.

Mainly a list of species belonging to the families Dysderidae, Clubionidae, Lycosidae, Agelenidae, Argyopidae, Linyphiidae, and Opiliones, from Laugharne, Carmarthenshire.

Sage, B. L. (1956). Notes on dragonflies in Wales in 1955. *Nature in Wales,* **2** (1), 220-224.

A list of species found in various Welsh counties, ranging from Carmarthen to Anglesey, and from the islands of Skokholm and Skomer.

Salmon, J. T. (1955). Two Collembola Symphypleona new to Britain. *Ent. Mon. Mag.* **91,** 241-242.

Sminthurides parvulus and *Metakatianna anglicana* sp. n. were both found in moss in a wood in Warwickshire. This is the first record of the genus *Metakatianna* in the northern hemisphere.

Scudder, G. G. E. (1955). *Drymus sylvaticus* (F.) (Hem., Lygaeidae) and *Velia caprai* Tam. (Hem., Veliidae) in Pembrokeshire. *Ent. Mon. Mag.* **91,** 264.

D. sylvaticus is recorded from Pembrokeshire for the first time.

Scudder, G. G. E. (1955). *Sthenarus roseri* (H.-S.) (Hem., Miridae) new to Bedfordshire. *Ent. Mon. Mag.* **91,** 283.

This species occurred on willow.

Scudder, G. G. E. (1956). Heteroptera in Northamptonshire. *Ent. Mon. Mag.* **92,** 21.

Five species are recorded, of which four are new to the county.

Shaw, S. (1952). Some records of Laboulbeniales (Fungi) on Coleoptera. *J. Soc. Brit. Ent.* **4,** 116-117.

Shaw, S. (1956). *Chrestosema* Foerster and *Aglaotoma* Foerster (Hym., Cynipidae Eucoilinae) two genera new to Britain. *Ent. Mon. Mag.* **92,** 16-17.

C. antennale is recorded from Yorkshire and *A. codrina* from Yorkshire and Lincolnshire. Characters distinguishing them from other British related genera are included.

Shaw, S. (1956). On the occurrence of *Hylecoetus dermestoides* (L.) and *Lymexylon navale* (L.) (Col., Lymexylidae) in Lancashire and Cheshire. *J. Soc. Brit. Ent.* **5,** 172.

Smith, K. B. V. (1955). *Sympetrum flaveolum* (L.) (Odon., Libellulidae) in Herefordshire. *Ent. Mon. Mag.* **91,** 202.

A new county record.

Smith, K. G. V. (1955). Some additions to the Hemiptera-Heteroptera of Shropshire. *Ent. Mon. Mag.* **91,** 237.

Contains 7 additions to the county list and some additional localities in Shropshire for four other species.

Smith, K. G. V. (1955). Thrips on the stinkhorn fungus (*Phallus impudicus* Pers.). *J. Soc. Brit. Ent.* **5,** 109.

Five species were found on an old fungus exposed to sunlight.

Smith, K. G. V. (1955). A second British record of *Myopa occulata* Meig. (Dipt., Conopidae) with notes on related species in the genus. *J. Soc. Brit. Ent.* **5,** 124-126.

A male was swept from rough herbage at Breamore, Hants., in 1948.

Steel, W. O. (1955). *Bohemiellina paradoxa* Machulka, a Staphylinid (Col.) new to Britain. *Ent. Mon. Mag.* **91,** 296-297.

This beetle was taken in Kent and Cambridgeshire. A description of the adult is included.

Underwood, R. (1955). *Servillia ursina* Mg. (Dipt., Tachinidae) in North Lancashire. *Ent. Mon. Mag.* **91,** 257.

A new county record.

Watts, W. J. (1955). *Hydroporus marginatus* (Duft.) (Col., Dytiscidae) in Essex. *Ent. Mon. Mag.* **91,** 252.

A new county record.

Whalley, P. E. S. (1955). Notes on some Homoptera Auchenorhyncha found in Caernarvonshire and Anglesey. *Ent. Mon. Mag.* **91,** 243-245.

A list, incorporating an earlier one by another author, of species, many from reed swamps, with dates, localities, habitats and food plants.

Yarrow, I. H. H. (1954). *Ancistrocerus gazella* (Panzer) (= *A. pictipes* Thomson), an abundant but hitherto undetected Eumenine wasp in Britain. *J. Soc. Brit. Ent.* **5,** 78-82.

The species is common in the south of England.

Yarrow, I. H. H. (1955). *Andrena combinata* Christ (Hym., Apidae): a bee new to Britain. *Ent. Mon. Mag.* **91,** 234-235.

Includes characters distinguishing this bee, found in Dorset, from *A. dorsata*, the only British species with which it could be confused.

Yarrow, I. H. H. (1954). Some observations on the genus *Bombus*, with special reference to *Bombus cullumanus* (Kirby) (Hym. Apidae). *J. Soc. Brit. Ent.* **5,** 34-39.

Lists the present known distribution of this bee.

Yarrow, I. H. H. (1954). *Colletes halophila* (Verhoeff) (= *C. succincta halophila* Verhoeff), a bee hitherto unrecognized in Great Britain. *J. Soc. Brit. Ent.* **5,** 39-41.

Yarrow, I. H. H. (1954). *Psenulus schencki* Tournier, a Psenine wasp new to the British list. *J. Soc. Brit. Ent.* **5,** 41-42.

Three females have been found in Surrey: the species has hitherto been recorded not nearer than Switzerland.

6. STUDIES ON BEHAVIOUR

Andrew, R. J. (1956). Begging responses of certain buntings. *Brit. Birds*, **49**, 107-111.

Describes begging responses of nestling yellow-hammers, reed and corn buntings, and their development, also the development of fear responses. The observations were mainly of hand-reared birds.

Armstrong, E. A. (1956). The amateur and the study of bird display: suggestions for further work. *Brit. Birds*, **49**, 97-106.

Reviews types of display, and suggests what data should be recorded by observers, and what species are of special interest.

Hinde, R. A. (1955, 1956). A comparative study of the courtship of certain finches (Fringillidae). *Ibis*, **97**, 706-745; **98**, 1-23.

The aggressive and courtship behaviour in captivity of eight species of finches studied in detail.

Meinertzhagen, R. (1955). The speed and altitude of bird flight (with notes on other animals). *Ibis*, **97**, 81-117.

A great number of records, published and unpublished, have been collected and tabulated.

Meinertzhagen, R. (1955). The effects of model scorpion and lizard on a bird-table. *Brit. Birds*, **48**, 556-557.

Birds in a London garden, including carrion crows and jays, all showed alarm when the scorpion was on the table but ignored the lizard.

Peterle, T. J. (1955). Notes on the display of the red grouse. *Scot. Nat.* **67**, 61-64.

Raines, R. J. (1955). Winter habits of ruffs. *Brit. Birds*, **48**, 545.

In three localities where ruffs winter they frequent very soft mud in late summer, and change their habitat suddenly and almost completely in late September or October to meadows and plough.

Smith, D. Summers- (1955). Display of the house-sparrow *Passer domesticus*. *Ibis*, **97**, 296-305.

Seven types of display other than communal are described, and pair formation and some aspects of behaviour are discussed.

7. REPORTS OF ORGANIZATIONS

Magazine of the Blundell's School Science Society (1954-55). No. 10, 36 pp.

Contains weather summary, brief reports on bees and the buzzard survey, and articles on comparative catches with mercury-vapour light traps at 80 feet and at ground level (P. S. Harper), and on absorption of light under water (M. J. Currie *et al.*).

Devon Bird-watching and Preservation Society (1956). Twenty-eighth Report, 1955. 80 pp.

Contains its usual features of an annotated systematic list of birds occurring in the county, reports on the black redstart and spotted flycatcher, enquiries and reports on the Chapel Wood bird sanctuary and the monthly wildfowl counts.

Essex Bird-watching and Preservation Society (1956). The Essex Bird Report, 1955.

Contains its usual features of an annotated systematic list of birds occurring in the county, and reports on the Bradwell Observatory, the Romford Ringing Station, and the monthly wildfowl counts ; also a short paper on the flooding of Hanningfield Reservoir.

Fair Isle Bird Observatory (1955). *Bulletin*, **2** (6), 237-284; (7), 285-332.

In addition to the usual records of bird migration on Fair Isle, other Scottish islands, and elsewhere in western Europe, these two numbers of the *Bulletin* contain several papers on flat-flies and bird-fleas, and a note on heavy mortality among eider ducks in Aberdeenshire.

Glasgow and West of Scotland Bird Bulletin (1954-55). **3** (4), 49-72; (5), 73-80; **4** (1), 1-12; (2), 13-24.

These bulletins contain numerous papers on the birds of various parts of the west of

Scotland, including the island of Pladda, North Rona, the Helensburgh district, Canna, Lady Isle and Baldernock parish in Stirlingshire; also on the game-birds of Arran and the censuses of the gannets of Ailsa Craig for 1952, 1953 and 1954.

Lancashire and Cheshire Fauna Committee: 30th Report (1954). 78 pp.

Contains records with localities and notes of mammals, reptiles and amphibians, 1949-51 (N. F. Ellison), whooper swans in southern lakeland and north Lancashire (A. F. Airey), inland gull roosts in Cheshire, and Cheshire rookeries (A. W. Boyd), opisthobranch molluscs, and Amphipoda in Cheshire (N. F. McMillan), Lepidoptera 1950-53 (H. N. Michaelis), additions to insect lists, 1950-51 (S. Shaw) and Rotifera, 1950-53 (A. L. Galliford).

BRITISH ECOLOGICAL SOCIETY

AUTUMN MEETING AT LONDON

19-20 September 1955

The autumn meeting was held in the Department of Botany, Bedford College, London, by courtesy of Professor L. J. Audus.

Monday, 19 *September* (11 a.m.) was devoted to a group of papers dealing with various aspects of the ecology of *Calluna vulgaris*. Professor A. R. Clapham was in the chair.

The first paper was by Mr R. A. Robertson on Scottish Calluneta.

While reseeding and pasture renovation are playing a large part in increasing the productivity of hill land in Scotland, the methods are costly and must be confined to relatively small areas on the lower slopes. Hence serious attention is being directed towards a better management of the natural hill pastures so that maximum output may be obtained and maintained.

Analyses of rumen and faecal contents together with feeding and digestibility trials, point to the value of heather (*Calluna vulgaris*) as an important constitutent of the diet of Blackface sheep. It is also known that this plant is an important source of certain trace elements (copper and cobalt) and this fact may be correlated with the absence of certain deficiency diseases in heather areas.

Further it is clear that the economic and social conditions over the past one hundred years have led to a deterioration of hill pastures with a consequent reduction in heather acreage and an increase in undesirable species such as bracken (*Pteridium aquilinum*) and white bent (*Nardus stricta*). Hence synecological and autecological studies of these upland communities and their species must be actively pursued in order that we may attain maximum output compatible with successful maintenance of productive swards.

A number of slides were shown to illustrate a few well-defined communities which are representative of much of the Scottish upland grazings. The climatic, edaphic, topographic and biotic factors concerned in their distribution were discussed.

The fact that heather occurs either as a dominant or an abundant species in most of these communities is evidence of its wide tolerance. It ranges from the pioneer communities of coastal dunes to the mature 'moorland' communities inland. The adaptation of *Calluna* to a wide range of habitat conditions is accompanied by a marked plasticity in its growth form.

In a broad survey of Scottish hill sheep farms an attempt is being made to relate productivity in terms of stocking rates, wool output and lamb crops to the type of vegetation and the management practices in operation and to determine the part which heather plays in hill land economy.

Experimental work is in progress to determine the effect of grazing wether sheep on enclosed areas of Calluneta of different ages. Broadly speaking the results of vegetation analyses and live-weight records indicate that a much shorter burning rotation than is generally adopted might increase the value of heather swards provided that the ability of the heather to regenerate is not impaired by too frequent firing. The experiment also indicates the preference which the sheep have for certain species at different times of the year.

Finally a short illustrated account of some problems of heather management was presented. Management to all intents and purposes is synonymous with burning although drainage is also an important factor. Regeneration of heather, seral development and the competitive power of subsidiary species were mentioned. In addition attention was drawn to the importance of controlling the heather beetle (*Lochmaea saturalis*) and the horse-hair fungus (*Marasmius androsaceus*).

Mr I. A. Nicholson then gave his paper on the characterization of Calluneta.

Extensive areas of Scottish hill grazings are composed of Calluneta. Grazing animals do not exert a uniform pressure on all communities forming the mosaic of vegetation over which they range. Palatability and availability of herbage vary with season and differ within each community, resulting in seasonal preferential grazing, while the relative areas of component communities are important in determining the extent to which each is subjected to biotic influence. In this way, modification to a given community reacts through biotic influence on others, forming a complex system of action and reaction within the whole enclosure.

Calluna is the dominant of many different communities over a wide range of conditions. In north-east Scotland, a study of four contrasting types of Calluneta in the mature phase, which in that area is reached between eight and twelve years after burning, showed marked differences in floristic composition and community structure. *Calluna* itself varied in height from 8 to 45 cm. and displayed growth-form differences resulting partly from differential frequencies of flower production, while in the types having closed canopies, shoot density varied from 378 to 1167 per $\frac{1}{4}$ m.^{2} Marked differences occurred in life form of associated species and in the floristic composition of succesive layers in each type. In the study of hill grazings, such differences and their significance should be fully recognized in relation to grazing behaviour and biotic influence.

When working with relatively large areas for experimental purposes, as in grazing studies, the variations in Calluneta cause difficulty in characterization and mapping. Methods of assessment sufficiently sensitive to reflect vegetation changes at intervals are required, without recourse to detailed land survey. On aerial photographs, the principal vegetation types are clearly delineated, but the variants in Calluneta cannot be differentiated. By point sampling along permanently marked transects at regular intervals over the area and by superimposing a 'point' map constructed from the data upon the aerial photograph, variations in the floristic composition of the Calluneta can be ascertained. The usual methods of vegetational analysis can be used on small sample areas to provide more detailed information.

In reply to Dr Conway, Mr Robertson said that the altitudinal range of Callunetum in the north-east of Scotland was between 600-1500 ft O.D. *Calluna* regenerates better from stools in *Sphagnum* in the west of Scotland. It was mentioned that in the drier parts of Britain establishment from seed was more effective. Mr Robertson stated that competition between seedlings was considerable; for example 1800 seedlings may be present in $\frac{1}{4}$ square metre. From these, forty plants may be established.

The effects of burning heather was discussed. Professor Clapham referred to the development of Vaccinietum after burning of a community of *Calluna* associated with *Vaccinium*. Dr Rose considered that the rhizomatous habit of *Vaccinium* favoured its rapid re-establishment following burning. Several members of the Society took part in a lively discussion, including Drs Gimingham and Leyton.

The afternoon session was opened by Dr C. H. Gimingham, who spoke about the growth forms of *Calluna*.

Interest in the management of heather moorland has revealed a lack of adequate information on the factors determining growth-form in *Calluna*. The structure of communities dominated by heather cannot be interpreted until full accounts are available for the forms adopted by individuals of different ages, in a variety of habitats.

Vigorous, uneven-aged Callunetum presents a pattern of individuals at different phases in their growth-form development, to which A. S. Watt applied the terms Pioneer, Building, Mature and Degenerate. The morphological basis for this sequence lies in the annual cycle of shoot formation. During the pioneer and building phases active growth takes place in 'long shoots', on which vegetative 'short shoots' are produced, both below and above a flowering region. New 'long shoots' are formed each season from 'short shoots' of the distal group, above a bare portion of stem representing the previous flowering region. This 'storeyed' growth leads to a hemispherical form, since the density of peripheral branches is maintained as the diameter of the bush expands. Any habitat factor affecting the extent of the flowering region will affect growth-form.

When about 15-20 years old, branches in the erect position produce shorter flowering regions and growth increments are reduced, with the consequence that short shoots appear

in closely superimposed clusters. This phase of 'maturity' ends as the centre of the bush opens out with a gradual falling apart of these erect branches, leading eventually to death of the oldest parts at the 'degenerate' stage.

Such changes in growth-form are reflected in the micro-climatic conditions below the plant. Measurement of light intensity showed steep gradients, from about 75 per cent. illumination in the central gap to less than 1 per cent at the periphery. Similar gradients in air humidity, temperature and soil factors are to be expected and may be inferred from the zonation of associated bryophytes.

The effects of other factors, such as edaphic influences, grazing and fire, upon growth-form arise from the modifications they impose upon the pattern of development described.

In the discussion Dr Rutter referred to the retardation of the growth of *Calluna* under dry conditions. Extension growth was larger near walls. Others who took part in the discussion were Dr T. Huxley, Dr A. S. Watt, Miss Frost, Mr Robertson and Mr Lavender.

The Calluneta of the central Cairngorm Area were then described by Dr G. Metcalfe.

The survey of 'Mountain Callunetum' between 2000 ft and 3000 ft on the northern slopes of the central Cairngorms (*J. Ecol.*, **38**, 1950) has been extended by observations on the southern slopes of the range. In general the Callunetum on the southern slopes is similar to that on the northern slopes and the community can be described as a unit.

Individual plants are prostrate, the foliage of one plant overlying the bare basal branches of another to give a thin turf 5 to 20 cm. deep. Associated plants occur either as tussocks or as patches in the *Calluna* turf connected by straggling bare stems beneath the *Calluna*. The principal associates are, at lower altitudes, *Trichophorum caespitosum*, and at higher levels, *Empetrum hermaphroditum*. On the northern slopes, *Arctostaphylos uva-ursi* at lower altitudes and *Loiseleuria procumbens* at higher altitudes are equally characteristic associates but on the southern slopes these species occur much less frequently. *Arctostaphylos* and *Calluna* in competition show a cycle of dominance, and the same cycle is evident in the recolonization of areas laid bare by disruption of the turf, and also in the colonization of areas step-terraced by solifluxion. At higher altitudes a similar cycle of dominance can be traced between *Calluna* and *Empetrum*, particularly on sloping or step-terraced ground.

The interaction of the vegetation with the habitat factors of exposure, snow cover and dampness is expressed by variation in the luxuriance of the *Calluna* and in the abundance of the associated species. It is particularly well shown by the zonation of facies on the platforms of large terraces, where the gradient of decreasing snow cover, decreasing moisture and increasing wind exposure is accompanied by a vegetational sequence of *Nardus-Vaccinium*, *Vaccinium-Empetrum-Calluna*, *Calluna-Empetrum*, *Calluna turf*.

On the brows of terraces and elsewhere, under conditions of extreme wind exposure (with which is associated rain-erosion of soil surface, especially at higher altitudes) *Calluna* occurs as isolated plants or groups of plants often showing unilateral growth. Characteristic associates disappear except for species (e.g. *Juncus trifidus*, *Empetrum hermaphroditum*, *Rhacomitrium lanuginosum*) dominant in the communities above the zone of Callunetum.

The upper altitudinal limit of the community is ill-defined, as interdigitation with the *Empetreto-Vaccinietum* occurs and ecotonal facies exist, but the transition is usually between 3000 ft and 3200 ft. In general, the Callunetum ascends higher on the more exposed sides of ridges than on the more sheltered sides.

Dr Poore said that growth habit was governed by wind exposure and the duration of snow cover. He also referred to the replacement of pine woods by a *Scirpus-Calluna* community. The role of solifluxion in determining the pattern of vegetation was mentioned by Dr Conway.

Two papers were read on the mineral nutrition of *Calluna* and its possible relation to tree growth. The first was given by Dr L. Leyton.

Certain tree species, particularly spruce, when planted on *Calluna*-dominated sites, usually make very poor growth; within a few years of planting the foliage becomes chlorotic and height increment is negligible. This so-called 'check' may be delayed but seldom completely avoided by ploughing and fertilizing with basic slag. Besides the inherent infertility of heathland and soils (base-deficient, very acid), conditions appear to be aggravated by the *Calluna* itself. This is supported by the following observations, (1) the onset of

check often coincides with the re-invasion of the site by *Calluna*, (2) in mixed plantations, growth of spruce improves rapidly when the nurse trees, e.g. pine, form canopy and suppress the *Calluna* by shade, (3) no comparable check occurs where *Calluna* is replaced by grasses or herbs, (4) removal of the *Calluna* by screefing results in a marked though temporary recovering in tree growth. The growth of pines also appears to be depressed by *Calluna* but to a much smaller extent than that of spruce.

Investigations into the mineral nutrient relations of spruce suggest that growth in the presence of *Calluna* is limited primarily by severe nitrogen deficiencies. Improvements in growth and in the N status of the trees have been obtained by (1) the direct application of nitrogenous fertilizers, (2) interplanting with legumes, e.g. broom, (3) suppressing the *Calluna* by artificial shade, and (4) mulching with *Calluna* shoots. Whilst a possible toxic influence of *Calluna* cannot be ruled out, the common rooting habits of spruce and *Calluna* in the same raw humus horizon suggest particularly severe competition between these two species, especially for the limited amount of nitrogen available. Observations that, in some areas, the growth of spruce can be correlated with the N status of *Calluna* plants growing in the vicinity of the trees, suggests a possible use of the *Calluna* as an indicator of site potentialities for tree growth.

The second paper was given by Mr J. R. Aaron on the mineral nutrition of *Calluna* and its possible relation to tree growth.

The relative luxuriance of *Calluna* is sometimes used in forestry practice to assess the fertility of planting sites and thus anticipate the success of schemes for afforesting heathlands. That is to say that better tree growth can be expected on a site which supports tall *Calluna*, than one which supports undersized *Calluna*.

Tissue analysis of dwarf *Calluna* (i.e. about 9 inches tall) growing as sole dominant and of well-developed *Calluna* (i.e. about 20 inches tall) growing as co-dominant with *Pteridium*, suggests that the difference is almost certainly a reflection of its nitrogen nutrition. The nitrogen content of the foliage of the luxuriant *Calluna* (expressed as a percentage of its dry weight) is about 57% higher than in the undersized *Calluna*, whilst the per cent dry weight of both phosphorus and potassium are only about 24% higher. In any case the saturation level for the uptake of potassium is about 0.1% of the dry weight – a level which is often found in undersized *Calluna*. As might be expected the percentage ash content of the foliage is greatest in the undersized plants.

The concentration of the nutrients varies considerably throughout the year. The optimum concentrations of potassium and phosphorus are observed during May, and this is to some extent reflected in the ash content which is also highest during May. The nitrogen content on the other hand seems to be greatest during March or April. When two years' foliage are borne on one plant, i.e. during late spring and early summer, the new foliage has a higher nitrogen content than the old, but the difference between the well developed *Calluna* and the dwarf *Calluna* is still maintained.

It can be concluded that although the relative size of even aged *Calluna* is not of much use in determining the availability of potassium and phosphorus, it may be a better means of assessing available nitrogen for tree growth than soil analysis particularly if the species under consideration root in the same horizon as *Calluna*. Furthermore, in view of the fact that *Calluna* growing as a co-dominant with *Pteridium* gives the highest nitrogen content of any sampled so far, there may be grounds for the suggestion that *Pteridium* is an indicator of comparatively high nitrogen availability.

In the discussion that followed Dr Rutter said that nitrogen was most important for the growth of the pine on heathland. Replying to Professor Clapham, Dr Leyton said that preliminary data was available on the balance sheet of nitrogen metabolism of the pine Several other members of the Society took part in the discussion; these were Drs Rorison, Godwin, Gimingham, Gore and Professor Burges.

Tuesday, 20 *September*. The morning session (10.30 a.m.-12.30 p.m.) commenced with a paper by Dr M. E. D. Poore on the advantages and limitations of the Braun-Blanquet system in descriptive ecology.

A critical but sympathetic review is needed of the work of the Braun-Blanquet school on the description and classification of plant communities in order that its good points may be incorporated in Anglo-American ecological practice and the bad rejected.

If the historical development of Braun-Blanquet's thought is studied it can easily be seen how, starting in the natural and semi-natural vegetation of the Alps, he was led to accept the Association concept, to value floristics for distinguishing and understanding the tolerances of associations and to choose faithful species as the characteristic by which to classify associations.

The system may be divided into five stages: the choice of communities to be described; description; arrangement of the descriptions into association tables and the delimitation of associations; classification; and – for us the most important – the use of floristic lists as a key to understanding the ecology and distribution of the association. The first two were discussed last year. Of the remainder the third is important and the procedure is difficult to understand, because the definition of the association is ambiguous and the use of faithful species for characterization involves a circular argument. Classification is into an hierarchy: Associations (termination -etum) are grouped into Alliances (-ion); and higher units are the Order (-etalia) and the Class (-etea). The higher units are always in theory, but more seldom in practice, distinguished by faithful species. (The subdivisions of the Class *Vaccinio-Piceetea* and a synopsis of the classification of the alpine and sub-alpine vegetation of Norway were used as illustrations of the classification.)

Advantages of the system are these: an insistence that ecological studies should be carried out on well-characterized vegetation units; the choice of floristics as the basis of the classification of vegetation; the choice of uniform communities for description; and the use of the association table for analysing the habitat factors which differentiate communities. If extensive observations are available the tables may be used to eliminate the factors which may occasionally appear to differentiate two communities, although in fact they do not. In this way the probable cause of any vegetational difference may be identified by a process of progressive approximation. This technique may be used to analyse differences of any degree, but it may be necessary to alter the precision of description to fit the problem being solved.

On the other hand there is much to criticize. Braun-Blanquet takes the sacredness of the association concept as one of the premises of his system. But the definition he gives leads to an association which is ill-defined, and which becomes more difficult to maintain as the amount of descriptive data increases. It is suggested that it may be more useful and more realistic to take Gleason's view of the association: that it is a continuous variable both in time and in space; but to establish in this continuum points of reference (*noda*) which coincide with communities which are repeated frequently and with little variation. These may, perhaps, best be characterized by constancy and dominance (dominance itself is not enough) and will then correspond with the Scandinavian 'sociation'. But the degree of integration of *noda* (i.e. the degree of similarity of the communities which compose them) may be varied according to the purpose of study.

The hierarchical classification breaks down because the relationships of vegetation are multidimensional. The most reasonable (though necessarily imperfect) method of representing the relationships of vegetation units is a grid with axes corresponding to floristic variations in response to two or three of the most important habitat factors.

It is useful to understand how the Braun-Blanquet classification works in order that we may better understand the literature of his school, but the most valuable features which emerge from study of it are two techniques: those of distinguishing fixed points of reference with unambiguous definitions, and of using the comparison of unit site descriptions as a techniquefor studying the ecology of vegetation units. Study, not classification, is the aim.

Professor Goodall considered that for descriptive purposes the Braun-Blanquet system was satisfactory, but it made a false assumption of the existence of a uniform stand. Associations vary continuously with habitat. The choice of areas for recording purposes was criticized. The concept of the nature of the association preceded identification. The random recording of sites within a grid was recommended.

From the statistician's point of view, Dr Hughes criticized the variable size of the stand plots. The variation in vegetation in relation to habitat factor was stressed by Dr Watt. Professor P. W. Richards emphasized the importance of the study of structure and physiognomy of vegetation.

Professor Burges said that outside Europe it was difficult to apply the Braun-Blanquet system to descriptive ecology.

Dr Godwin stressed one important weakness of the Braun-Blanquet system, that is, insufficient attention to the mechanism of vegetational change.

Dr Hughes considered that it was more fruitful to describe vegetation in distinct habitats – this presupposed that a study and classification of habitats would precede that of the vegetation. Proceeding in this way a deeper insight is obtained of the major factors controlling the distribution of certain plant communities, and the process of change within the communities.

The afternoon session (2-4 p.m.) was devoted to a paper by Dr E. W. Fager on the detection and analysis of species groupings.

When dealing with animals which are difficult to observe directly and which, must, therefore, be studied by sampling, it is helpful to have some method of grouping species. The method will be most useful if it puts together those species which form a nearly constant part of each other's biological environment. It should be based on an explicitly defined measure of the tendency of species to form mixed populations so that subjective elements are reduced as far as possible. As measures which involve abundance do not always lead to the desired results, it seems best to use presence and absence only and to consider abundance relations within the groups after they have been formed. Cole's (1949) coefficient of association has often been used but it is unsatisfactory as a basis for grouping for two reasons. Under certain circumstances it fails to give evidence of affinity between species which nearly always occur together and under others it indicates significant affinity when the species are rarely found together. These difficulties arise because of the assumption that the total number of samples taken in the study is the correct estimate of the number of samples over which the two species being tested for association were distributed. This is the reason for the excessive number of positive associations found by Macan (1954) in his study of British Corixidae.

A new measure of affinity is suggested which takes account of all numbers of joint occurrences which are possible between two species with the observed frequencies. The measure is sensitive to the total number of samples on which it is based and to the proportion between the numbers of occurrences of the two species. It minimizes the chance of finding significant evidence for affinity when there is none. It is based on the assumption that the sum of the total number of occurrences of the two species is a valid estimate of the number of samples over which they were distributed. On this assumption, the number of joint occurrences will be distributed nearly as a binomial and a test of the significance of the deviation of the observed number of joint occurrences from the expected number can be made using the normal approximation to the binomial. In order to use the approximation it is necessary to put limits on the relation between the frequencies of occurrence of the two species. These limits also ensure that any affinity found will be of importance to both of the species concerned.

If a recurrent group is defined as one within which all pairs of species show significant evidence of affinity, as the largest such group which can be formed from the sampling results and as the group with the greatest total number of occurrences if more than one of the same size can be formed, a procedure can be prescribed which will lead to a group with these characteristics. Although the finding of affinity between pairs of species and the grouping together of several species do not prove the presence of interspecific processes, the properties of a recurrent group, as defined, are such that it would be a likely choice if one wished to make an intensive study of interspecific processes which are quantitatively important in the habitat.

It was suggested that ranking methods (Kendall 1955) are particularly appropriate for examining such inter-specific concepts as dominance, concordance and correlation within recurrent groups. Using such methods it is possible to test the significance and constancy of the relations observed. They are especially useful for selecting those samples which were the best and worst habitats for the group as a whole. These extremes may indicate the group's requirements in regard to various habitat features.

References

Cole, L. C. (1949). The Measurement of interspecific association. *Ecology*, **30**, 411-24.

Kendall, M. G. (1955). *Rank Correlation Methods*. London.

Macan, T. T. (1954). A contribution to the study of the ecology of the Corixidae (Hemipt.). *J. Anim. Ecol.*, **23**, 115-41.

In the discussion that followed Professor Goodall, Mr Skellam, Mr Norman, Professor Richards, Mr Harberd, Dr Williams, Dr Hopkins, Dr Wall, Dr Poore and Dr Hughes took part.

The President concluded the Meeting by thanking all who had taken part and also Professor Audus and Dr Francis Rose for their hospitality and help in its organization.

R. ELFYN HUGHES

THE ANNUAL GENERAL MEETING

5-7 January 1956

The 37th Annual General Meeting of the Society was held in the Department of Botany, Oxford, by kind invitation of Professor Darlington.

On the evening of 5 January a soirée was held in the Department of Botany, at which a wide range of exhibits were shown illustrating the ecological work in progress at Oxford.

Professor Gordon, of New Zealand, was able to show the Society an excellent series of coloured slides of New Zealand vegetation.

The Annual General Meeting, 5 January, started at 10 a.m. In the absence of the President, Captain C. Diver took the chair.

Apologies for absence were received from Professor Clapham, Mr Holdgate, Dr Godwin, Mr Chear, Mr Johnston and Dr Watt.

1. *Minutes of the last Annual General Meeting, 8 January 1955*

On the proposal of the Chairman, the Minutes of the last Annual General Meeting held on 8 January 1955, at the Department of Zoology, Imperial College of Science and Technology, South Kensington, London, were taken as read, as they had already been published in *J. Ecol.*, **43**, p. 672 and *J. Anim. Ecol.*, **24**, p. 517.

The Report of the Honorary Secretaries for the year 1955 was read by Dr R. E. Hughes.

2. *Report of the Honorary Secretaries*

On 8 January 1955, the 36th Annual General Meeting of the Society was held at the Department of Zoology of the Imperial College of Science and Technology, South Kensington, London.

On the evening of 7 January a soirée was held in the Department of Zoology, at which Professor O. W. Richards and his colleagues had set out a range of exhibits illustrating work in progress in his department. During the soirée an excellent film was shown by Dr J. A. Kitching of ecological work in progress on the Lough Ine rapids.

At 10.30 a.m. on 8 January the Annual General Meeting was held at the Department of Metallurgy. The President, Professor A. R. Clapham, was in the chair. An account of this meeting has appeared in *J. Ecol.*, **43**, 672, and *J. Anim. Ecol.*, **24**, 512. At 11.30 a.m. Professor Clapham delivered his Presidential Address entitled 'Autecology and the Biological Flora'.

During the afternoon, the following papers were read:

J. MacLeod: Field populations of Calliphorine flies.

G. Orshan: The vegetation of Israel.

O. W. Richards and M. Waloff (delivered by Dr. Waloff): The study of a population of a beetle (*Phytodecta olivacea*) living on broom.

The Society is grateful to Professor Richards and his staff for their hospitality and excellent arrangements for the meeting.

The Easter Meeting, 29-31 March 1955, was held at the Departments of Zoology and Botany at Durham University by kind invitation of Professors J. B. Cragg and D. H. Valentine.

Accommodation was provided at Lumley Castle where on the evening of the 29th members of the University staff and the Society foregathered and spent a most enjoyable evening.

Wednesday, 30 March, was devoted to the ecology of the Moor House area. The meeting started at 10 a.m. with Professor Clapham in the chair. The following papers were read:

V. M. Conway: Introduction.
J. B. Cragg: Zoological investigations in progress at Moor House.
D. H. Murphy: The Collembolan fauna of moorland and its relationship to bog growth and degeneration.
J. A. Svendsen: Studies on the earthworms associated with sheep dung at Moor House.

During the afternoon three further papers were read:

A. M. Jordan: Population studies on *Coleophora caespitiella* Zell. in relation to its food plant, *Juncus squarrosus* L.
V. M. Brown: Ecological studies on the stoneflies (*Plecoptera*) at Moor House.
C. D. Pigott: Calcareous marshes in Upper Teesdale.

At 4.30 p.m. tea was provided in the Department of Botany, and an excellent range of exhibits were available showing the work in progress in both the Departments of Botany and Zoology.

Thursday, 31 March, was devoted to a symposium on the Ecology of Soil and Litter Fauna and Flora. The following papers were read:

C. Overgaard-Nielsen: The fauna of mull and mor.
W. Kühnelt: On the water relations of soil animal communities.
N. A. Burges: The concept of the community in soil microbiology.
M. A. M. Kharbouch and J. Webster: Decomposition rates of fungi in soil profiles under *Holcus mollis* and *Deschampsia flexuosa*.

The meeting was outstandingly successful, and the Society is much indebted to both professors and the staff for the arrangements made and their hospitality.

The Summer Meeting (16-21 July 1955) was held at the University Department of Botany of Old Aberdeen by kind invitation of Professor J. R. Matthews.

On the first day there was an excursion to beech woods at Hazlehead and a soirée in the Department of Botany.

The second day was devoted to an interesting excursion to the sands of Forvie, where a number of fine dune ridges in different stages of colonization were crossed and several interesting communities and species seen.

On Monday, 18 July, the meeting went up Deeside to Creag-an-Dail Bheag. Here a rich alpine flora was explored.

The fourth day opened with a discussion on *Calluneta* in north-east Scotland, when papers read by Dr Gimingham, Dr Robertson and Mr Nicholson stimulated a lively discussion. In the afternoon the experimental farm at Glensaugh was visited to see various *Calluneta* and experiments in their management.

On Wednesday, 20 July, the Society visited the cliffs, dunes and salt marsh at St. Cyrus, where the salubrious environment and rich flora were much enjoyed. In the evening a discussion on *Myxomatosis* was held at Milton Hostel. Dr Thompson, Dr Morison and Dr Hope-Simpson spoke on the spread of the disease and its effect on the British fauna and flora and a stimulating informal discussion resulted.

On the last day visits were paid to the Macaulay Soil Institute, the University Department of Zoology and the Marine Laboratory, where interesting demonstrations of research in progress were seen.

The Society is grateful to all its hosts in Aberdeen and especially Dr. Gimingham for such an enjoyable and stimulating meeting.

The Autumn Meeting of the Society was held at the Department of Botany, Bedford College, Regent's Park, London, by courtesy of Professor L. J. Audus.

Monday, 19 September, was devoted to a group of papers on *Calluna* and *Calluneta*. Professor Clapham took the chair. The following papers were read:

R. A. Robertson: Scottish Calluneta.

I. A. Nicholson: Characterization of Calluneta.

C. H. Gimingham: Growth forms of *Calluna*.

G. Metcalfe: Calluneta of the Central Cairngorm area.

L. Leyton and J. R. Aaron: The mineral nutrition of *Calluna* and its possible relation to tree growth.

At 8.30 p.m. a soirée was held in the Department of Botany.

On Thursday, 20 September, two papers were given dealing with aspects of the problem of the classification of communities of living organisms. In the morning, at 10.30, Dr M. E. D. Poore read a paper entitled 'The advantages and limitations of the Braun-Blanquet system in descriptive ecology'. In the afternoon, Dr E. W. Fager dealt with the statistical approach to the problem with particular reference to animal communities. His paper was entitled 'The detection and analysis of species groupings'. Each paper was followed by a very lively and useful discussion.

The Society is indebted to Professor Audus for his hospitality and to Dr F. Rose for local arrangements for this meeting.

During the year two parts of the *Journal of Ecology*, Volume **43** have appeared. No. 1 has 387 pages, comprising 23 original articles and 6 book reviews. Included were 4 accounts of the Biological Flora of the British Isles; they were: *Erica mackaiana* Bab. by D. A. Webb, *Narcissus pseudonarcissus* L. by John Caldwell and T. J. Wallace; *Nuphar* Sm. by Yolande Heslop-Harrison; and *Thymus* L. by C. D. Pigott.

No. 2 has 345 pages, comprising 13 original articles, 9 book reviews, accounts of meetings of the Society for the year 1954, and the Annual General Meeting, January 1955. Three accounts of the Biological Flora appeared; they were: *Vaccinium vitis-idaea* L. by J. C. Ritchie, *Succisa pratensis* Moench, by A. W. Adams, and *Nymphaea* L. by Yolande Heslop-Harrison.

Two parts of Volume **24** of the *Journal of Animal Ecology* have appeared. No. 1 with 254 pages, containing 9 original articles, and book reviews. No. 2 with 285 pages, containing 12 original articles and 9 book reviews. Both numbers contain abstracts of scientific papers with bearing on the animal ecology of the British Isles.

An analysis of membership is as follows:

Total	Receive *E.* only	Receive *A.* only	Receive *A.*+*E.*	Associate members	Hon. members
934	490	261	169	14	4

Distribution:	Home	665
	British Commonwealth	154
	Foreign	125
		934

The total membership of the Society has therefore increased during 1955 from 879 to 934, that is by 55.

The Secretaries regret to report the death of Sir Arthur Tansley, F.R.S., a founder member of the Society, and in turn Secretary and President of the Society, for many years Editor of its Journal and afterwards honorary life member.

In conclusion, the Secretaries wish to draw the attention of the Society to our continued increase in numbers. Also, as a reflection of this progress and the increase in ecological research in Britain, it has been possible during the past few years to expand the activities of the Society. First of all by the introduction of a two-day Easter Meeting, followed by an Autumn Meeting usually of one-day duration. During the past year the latter meeting was extended to two days, and the Annual General Meeting into a second day.

It is considered that further expansion should take place as it is not now possible to accept all papers which are offered by our members for various meetings. The Secretaries hope that this situation will be rectified in the near future.

3. *The Report of the Honorary Treasurers*

The Honorary Treasurers' Report was read by Mr V. S. Summerhayes. A full statement of his account will appear in both Journals during 1956; it is enough to record here that the Society worked to a surplus of approximately £200.

4. *The Election of Officers and Members of Council*

The Society then proceeded to the election of the Council and its officers, and the following were elected:

President: G. C. Varley.
Vice-Presidents: C. R. P. Diver, N. A. Burges.
Honorary Secretaries: C. H. Gimingham, E. D. Le Cren.
Honorary Treasurers: C. E. Hubbard, V. S. Summerhayes.
Honorary Editors: H. Godwin, H. C. Gilson.

Council:
P. F. Holmes (1960), R. E. Hughes (1960), T. T. Macan (1960), D. A. Webb (1960), M. W. Holdgate (1957), V. M. Conway (1957), J. B. Cragg (1957), N. W. Moore (1957), H. B. N. Hynes (1958), O. W. Richards (1958), P. W. Richards (1958), F. H. Whitehead (1958), J. H. Barret (1959), E. M. Burrows (1959), D. E. Coombe (1959), J. F. Hope-Simpson (1959).

Dates refer to year of retirement.

Honorary Editors of the Biological Flora: A. R. Clapham, H. Godwin, P. W. Richards
Honorary Assistant Editor: D. E. Coombe

Professor Varley, as the new President, then took the chair.

5. *The Reports of the Honorary Editors*

(*a*) *Journal of Animal Ecology*. Mr Gilson referred to the change of publishers from the Cambridge University Press to Blackwell Scientific Publications, Ltd., of Oxford. It was estimated that there was a delay of 15-18 months in the publication of articles. A solution would be to increase the size of the Journal, which would inevitably increase its cost.

(*b*) *Journal of Ecology*. Dr David Coombe referred to the substantial flow of papers for publication. Sixteen months was the minimum period of delay in publication. He asked for conciseness of presentation.

Both reports were accepted by the Society.

In the discussion Professor Webb considered that detailed records might be lodged elsewhere in some suitable institution for reference purposes. His views were supported by Mr Skellam. Dr E. W. Jones pointed out that it was difficult with descriptive ecological material to present the relevant scientific information in a short paper. Further, if a major work of this kind was split up into a number of short papers continuity was lost.

6. *The Report of the Honorary Editors of the Biological Flora*

Professor P. W. Richards reported that accounts were published in 1955 of ten species and one hybrid. He advised authors to consult the Editors at an early stage about their contributions. Preliminary drafts might be submitted to them.

Dr Noel Robertson, who had been responsible for supplying information on the fungal diseases of plants, dealt with in the Biological Flora, was no longer able to continue this work. Professor Richards expressed the thanks of the Society for the very considerable help that he had given.

At 11.15 a.m., after a short break for coffee, Dr W. B. Turrill (Royal Botanic Gardens, Kew) opened the session with a paper on 'Some ecological problems of the bladder-campions' as an example of synthetic methods applied to one group of plants and of the results thus obtained. At Kew and Potterne the speaker and E. M. Marsden-Jones have grown thousands of plants from seed of known wild origin and have scored families from 368 controlled selfings and crossings. In addition, populations have been studied in the field over much of the ranges of the two major species concerned, *Silene maritima* and *S. vulgaris*. About 25 groups of characters have been used and correlated researches in anatomy and cytology have been carried out by associated workers. The investigations as a whole are now being prepared for publication in book form.

The two major species, and the subspecies within them, are excellent examples of ecologically isolated taxa. There are genetical sterility factors within the group and even sometimes within the subspecies and within local populations but these, at least frequently, do not coincide with either taxonomic or ecological boundaries. Habit characters are considered as of very great importance in restricting taxa to given ranges of ecological conditions. Habit, however, is a complex and though, for example, lifeform, stem-height, and flower number are ecologically linked or associated they are genetically independent since the differences are controlled by separate gene systems.

The very interesting parallels in structure and behaviour between *Silene maritima* and *S. vulgaris* subsp. *alpina* and subsp. *glareosa* were discussed at some length. Sharply defined ecotypes occur in the Alps and though some characters, such as those of 'habit' are obviously correlated with habitat conditions, others would seem in themselves to have no known survival value. Thus, the plants of *S. maritima* on, for instance, the Chesil Beach and of *S. vulgaris* subsp. *alpina* on screes of calcareous schists opposite La Grave in Hautes Alpes have capsules with reflexed teeth and wide mouths and 'armadillo' seeds while lowland populations of *S. vulgaris* subsp. *vulgaris* have capsules with erect or slightly spreading teeth and narrow mouths and tubercled seeds. On the other hand, inland populations of *S. maritima* have entirely or predominantly tubercled seeds. A similar puzzle is to explain why *S. maritima* and *S. vulgaris* var. *alpina* have, at least predominantly and in some populations in almost every plant, purple immature seeds, while *S. vulgaris* var. *vulgaris* of the inland lowlands has white seeds with very few exceptions.

It is suggested that the bladder campions are a virile group in process of further speciation by differentiation from a stock that was widespread in late Tertiary times. The oncoming of glacial conditions caused the selection of the ancestors of *S. maritima* in north-west Europe and of *S. vulgaris* subsp. *glareosa* and subsp. *alpina* in the Alps and of other subspecies in other parts of the range. It is probable that *S. maritima* survived the Glacial period in the British Isles but that *S. vulgaris* is of Post-glacial introduction or reintroduction.

In reply to Professor Varley, Dr Turrill said that pollination was carried out by bees and moths. Replying to Professor Richards the speaker said that both the tubercled and armadillo seeds were interglacial in occurrence. Several other members of the Society took part in the discussion: these included Dr Harper, Mr T. Pritchard, Professor Webb and Professor Valentine.

Professor D. H. Valentine then gave his paper on 'The relationship of genetics to ecology: problems and techniques'. In the first part of the paper, the approaches of the ecologist and the geneticist to problems of the biology of single species were contrasted. The differences were illustrated by the work of G. E. Blackman and his colleagues on the bluebell, in which the main emphasis was on physiology and autecology, and by the work of Clausen, Keck and Hiesey on various species in California, in which the main emphasis was on genetics. Current divergences of aims were illustrated by *Holcus mollis*, the autecology of which has been studied by Ovington and others, and the cytogenetics by Beddows and Jones; the advantages of a combined approach were pointed out. Attention was also drawn to the fact that genecologists have frequently neglected to interpret their results in relation to the structure of the plant communities concerned. The opinion was expressed that the development in Britain of a system of community classification of the type used by continental plant sociologists might place a useful tool in the hands of genecologists.

In the second part of the paper, the bearing of genetics on plant geography was illustrated by reference to the flora of New Zealand. Such evidence as is available indicates that this

flora contains a number of coenospecies (e.g. in the genera *Hebe*, *Coprosma* and *Epilobium*) each consisting of groups of gradual-ecospecies (homoploid species capable of limited gene-exchange). Such groups are generally considered to have originated allopatrically, and the problem arises of their mode of origin in New Zealand, which is a relatively small land mass, isolated from other land masses by ocean barriers for a very long time. Sympatric speciation is a possibility, given a sufficient diversity of climate and habitat maintained for a long enough period; and partial submergence during the Tertiary to produce a group of smaller islands may have been an important factor. As another possibility, the theory of successive invasions, at long intervals of time, was mentioned; this has been put forward to explain similar phenomena in birds. A widely based investigation of two or three of these coenospecies in New Zealand along the lines suggested might not only clear up the questions at issue, but also throw light on general phytogeographical problems in this area and elsewhere.

In the discussion that followed, Professor Gordon, of New Zealand, stressed the climatic diversity there which might lead to ecological separation of populations.

The afternoon session was opened by Professor C. D. Darlington, who gave a very stimulating address on 'Ecology and the breeding system'.

The best starting point for considering the relations of genetics and ecology has been the natural population, a unit to some extent ecologically adapted and to some extent genetically isolated. The natural population is interfertile and constitutes a breeding group. The exchange of genes within such a breeding group allows us to speak of it genetically as a 'gene-pool'.

This situation does not occur so often as it would appear to do. The classical view of gene-exchange depends on the view that all chromosomes have to cross over in order to form chiasmata, to pair, and to contribute to fertile germ cells and progeny. But this ideal situation is complicated by the nature of variation.

Variation occurs not only by gene mutations affecting the character of the individual but also by others affecting the breeding and reproductive system of the race. And also by gross changes in the chromosomes themselves. In short-lived flowering plants the following proportions of species probably contain such aberrations in some stage of development.

Accessory or B chromosomes	10 per cent.
Floating Interchanges (giving *Oenothera systems*)	20 per cent.
Apomixis	30 per cent.
Polyploidy	50-75 per cent.
Floating Inversions	90-100 per cent.

In animals the frequencies are lower at least for interchanges and polyploidy.

Gene mutations and chromosome changes of these kinds affect the breeding system by reducing the size of the breeding group or impeding the recombination of genes in the 'gene-pool'. Often the changed individual is at one stroke genetically isolated. Now populations are adapted to the size of the breeding group and the gene-pool. We can show this by the simple expedient of inbreeding an outbreeding species. Homozygotes we expect to be produced but their properties lead to utterly contrasted results. In *Secale cereale* there is a segregation of viable recessive types; these are either stable or most unstable. In *Campanula persicifolia* the homozygotes die and the result is to encourage complex hybridity on the *Oenothera* pattern. Facultative apomixis is another kind of result which appears in *Potentilla* (Rees (1955) and Darlington (1956), *Proc. Roy. Soc.*, B.).

The unstable types in *Secale* explain how chromosome changes may not only lead to changes in the breeding system but also follow from them. Certain consequences of this are seen from a study of plant geography. We find the greatest chromosome changes in a group in regions remote from the place of origin of the group. This is true (as Professor Darlington tried to show in *Chromosome Botany*) of changes in basic number, in polyploidy, and in the development of permanent hybridity.

It is as though genetic change is favoured by movement. It occurs on the moving margin. The colonizers are no doubt compelled to adapt themselves to new conditions. But part of this adaptation must be due to the continual pressure to reduce the size of the breeding group. Sequences of events may be encouraged in this way as diverse as polyploidy or

mutation to self-fertility. In *Oenothera* it appears that the habit of self-fertilization has been adopted as the species moved eastwards across North America and this in turn has led to the formation of hybrid species by the *Campanula* reaction to inbreeding.

This view of peripheral change seems to contradict Vavilov's observation that the greatest diversity in species of cultivated plants is found in certain central regions. In my opinion, however, Vavilov's 'centres' are not centres of origin but regions of ecological diversity: they are ecologically peripheral.

The interactions of environment and genotype (and of ecology and genetics) are thus complicated by the intrusion of a third variable, the breeding system, a variable which is itself ecologically and genetically controlled in very diverse ways. The comparison of these effects among animals which are mobile in an *individual* sense, so that the genotype can select the environment, and among plants which are mobile only in a racial or genetic sense, is already proving instructive.

In reply to Professor Valentine, the speaker said that less was known about aberration in the breeding and reproductive system in animals. Dr Turrill stressed the significance of number and size of chromosomes in the breeding system. In this connection Professor Darlington mentioned the specialized capacity of some polyploids for vegetative reproduction. Several other members took part in this discussion.

Dr E. B. Ford then gave his paper on the 'Experimental Study of Animal Populations'. He said that it is becoming clear that micro-evolution proceeds much faster than was realized twenty years ago. At that time, selective advantages of 1 per cent or so were considered to be high whereas, in fact, they frequently reach values of 20 to 30 per cent. That is to say, the importance of those factors which contribute to rapid evolution had until recently been underestimated.

Much attention has in the past been paid to instances of widespread fluctuations in numbers due to climatic cycles. These are relatively rare and unimportant compared with the fact that isolated populations generate marked numerical fluctuations autonomously as it were. These, herefore, are not synchronous from one colony to another but they greatly favour rapid evolution. When a population expands, the selective pressure is reduced and genes which would otherwise be held in check can spread. They can then be tried out in new combinations, some of which may be advantageous. These will be at a premium when the population is reduced once more under stricter selection; as originally shown in the butterfly *Melitea aurinia.*

Polymorphism contributes to rapid evolution owing to the high frequency at which both allelomorphs of the switch-gene, or super-gene, are maintained. As such a gene spreads, it will tend to acquire an advantage in the heterozygous state and so to produce polymorphism. Other genes which contribute to that advantage will tend to become closely linked with it. Consequently, polymorphisms are usually controlled by groups of super-genes often regarded at first as single units.

The subdivision of a population into small isolated units promotes its rapid evolution as each group can then be adjusted to the particular ecology of its locality, whereas a population occupying a large territory can be adapted only to the average of the conditions which obtain there. This situation is being studied in the butterfly *Maniola jurtina*, especially in the Isles of Scilly. Minor ecological barriers prove to be remarkably effective in isolating small groups, even of species possessed of great powers of dispersal. One hundred and fifty yards of unsuitable country is almost a complete barrier to *M. jurtina*, though in its own territory it can, and constantly does, fly this distance in a few minutes.

Replying to Professor Valentine, Professor Ford said that the variation in spot characteristics was not closely correlated with physiological characteristics.

The final paper of the day was given by Captain C. Diver on 'Populations and adaptability'.

Ecological adaptability is the antithesis of specialized adaptation. The former is one of the hallmarks of the successful species and enables it to occupy many varied conditions and different societies; while the latter tends to limit the species' range of tolerance.

The spatial distribution, or distributional pattern, of all natural populations is characterized by discontinuity; populated areas are separated from each other by unoccupied ground, and even in apparently continuous populations differences in the density of

individuals may be sufficient, in the less mobile species, virtually to isolate various groups. The degree of adaptability possessed by a species will affect the distributional pattern both of the populations, or colonies, within its geographical range and of the individuals within colonies.

In very general terms, the adaptable species tends to be common in the ecological sense with very many, and more widespread, colonies. It has better chances of remaining in the same place in spite of changed conditions, though such changes may modify the distributional pattern of the individuals within the colony. There is greater likelihood, because of the comparative density of the pattern, of the species spreading to other habitats that are or have become within its range of tolerance; and also of increased genetic interchange between colony and colony.

At the other end of the scale, increasingly specialized ecological adaptation leads to localization; fewer, and probably more isolated, colonies; decreasing chances of occupying new habitats and of genetic interchange between colonies; and greater likelihood of individual colonies being wiped out by the deterioration of their habitat.

The population pattern of a species represents a cross-section of a continuously altering passage through time as the species responds to a background that is always changing. The maintenance of a changing distributional pattern calls for some provision for dispersal; and another interesting antithesis presents itself – the capacity to move *versus* the desire to stay in the same place. The available evidence strongly indicates that most animals, whatever their potential mobility, do not voluntarily move away from their own area or habitat unless compelled to by adverse conditions. This voluntary restriction of movement by mobile species must impose checks both on colonization and on genetic interchange – checks which should be increasingly effective as mobility and suitability for involuntary transport decrease. Yet dispersal has been achieved and, given time, species do colonize new habitats within their tolerance range.

Captain Diver concluded by saying the system works: the question 'How?' remains open.

In the discussion that followed, in which several members of the Society took part, Dr Turrill dealt with the adaptability and plasticity of species. *Plantago media* showed great change with the kind of soil, while *Centaurea nigra* did not. Dr Yapp said that the barn-owl had a restricted habitat range, but had a widespread geographical distribution.

On Saturday, 7 January, the morning session opened at 10.15 a.m., the first paper being given by Mr I. H. Rorison on some physiological aspects of the calcicole-calcifuge problem.

Field and laboratory experiments involving two calcicoles. *Scabiosa columbaria* L. and *Asperula cynanchica* L. and two calcifuges, *Holcus mollis* L. and *Galium saxatile* L. were described. Their bearing upon some current theories on the problem were discussed.

Within the limits of the species and soil types used, it was found that chemical factors, and in particular the presence or absence of calcium as calcium carbonate, were the prime factors in the complex interaction controlling the spread of the plants. These factors were most influential during a critical phase in seedling development and did not affect healthy transplants. The calcicoles germinated and developed well under alkaline conditions, but died as seedlings on the acid soil used (pH 4.8). Water cultures confirmed that death was accompanied by aluminium toxicity – closely associated with the failure of root initials to penetrate the cortex – and with phosphate deficiencies in the leaves. This condition was only remedied by raising the pH of the soil – most effectively by the addition of calcium carbonate.

The calcifuges thrived on this same acid soil, but failed under alkaline conditions due mainly to potassium, iron and phosphate deficiencies of which only the phosphate deficiency could be remedied by the direct application of nutrient.

Plant competition was shown to be of secondary importance in the seedling stage, but depressed strongly any later development.

Physical soil factors did not exercise any noticeable influence during the experiments described.

It was concluded for both the calcicoles and calcifuges examined that the presence or absence of calcium as calcium carbonate is the primary factor affecting the survival of these plants in the seedling phase. It is not considered to have a direct effect but that in maintain-

ing alkaline conditions it creates a suitable medium for a complex of interactions which either increases or decreases the availability of certain nutrients such as calcium, potassium, phosphorus, nitrogen, iron and aluminium to the various species.

The importance of field work in exposing critical factors which may be overlooked in the laboratory was stressed, and possibilities for more far-reaching physiological experiments involving individual species were suggested.

Dr E. W. Jones said that the survival of seedlings in turf was small, and would be influenced by its thickness. The low percentage germination of *Galium saxatile* was mentioned by Professor Valentine. Professor Webb, Mr E. D. Le Cren and Dr Turrill also took part in the discussion.

The second paper of the day was given by Mr C. H. Fernando on 'Ecological study of some Helophorid beetles'.

Five species of the Hydrophilid genus *Helophorus* (*H. aquaticus* (L.), *H. dorsalis* (Marsh), *H. flavipes* (F.), *H. brevipalpis* (Bedel), and *H. minutus* (F.)), colonize a variety of temporary aquatic habitats including ephemeral, temporary and permanent ponds.

They are difficult to observe in the field because their colour matches the mud closely and they burrow into the mud at the edge of ponds as they dry up.

H. brevipalpis, the most abundant species, is very common during the summer, whilst the other species are commonest during the spring and autumn.

Egg laying takes place from November to June, the overwintering females mate a second time in spring. Large larvae have been found in damp soil near water or in dried-up ponds where the soil is still moist during June and July. *H. brevipalpis* emerges as adults from June until the middle of August. Although soft, newly emerged *H. aquaticus* have been taken as early as July, the main emergence is from mid-August to September. The other species emerge in September and October.

Colonization was investigated at Wytham (Berkshire) and Cassington (Oxfordshire) using traps and artificial habitats.

H. brevipalpis emerge and disperse in large numbers during June, July and August, when climatic conditions are favourable for flight. Crowding and competition are probably important factors causing dispersal. The other species disperse little during this period as they emerge from the middle of August when climatic conditions are less suitable for flight. There is also very little crowding in these species. All the species disperse to a small extent in March, April and May when mating and egg laying takes place for a second time. This relieves congestion of the new generation by spreading it over a wider area.

Location of a habitat is by sight, the insects flying in nearly equal numbers to artificial habitats and glass traps both by day and night.

H. brevipalpis and *H. aquaticus* preferred muddy-bottomed artificial habitats to sandy and stony ones.

This investigation of the ecology of five species of *Helophorus* living in similar habitats throws light on certain properties of rare and common species. The commonest species, *H. brevipalpis*, has a high power of dispersal, emerging in large numbers when conditions are favourable for flight. The rare species disperse little, emerging in smaller numbers when conditions are less favourable for flight. Dispersal serves to extend both feeding and breeding grounds and prevents overcrowding.

Several members took part in a lively discussion. The problems of beetles finding small bodies of water and the experimental glass traps even at night evoked the most interest.

Mr J. K. Bates then gave his paper on 'Host selection in Bird Fleas'.

The immature stages of bird fleas are found only in the nests of their hosts. The nest as a habitat is peculiar in that there is a steep gradient of temperature and humidity from the warm and dry layers of nest material immediately below the bird to the outer layers of the nest.

Sixteen species of bird fleas are known to occur in the British Isles. The problem of host selection in the three common bird fleas were discussed, i.e. *Ceratophyllus gallinae* (hen flea), *C. garei* (duck flea) and *Dasypsyllus gallinulae* (blackbird flea). Each of these fleas has been recorded from about 50-60 hosts in the British Isles. Rothschild showed that the hen flea was usually found in the nests of birds which build in holes or some distance from the ground, the blackbird flea in nests near the ground and the duck flea in nests on the

ground. She suggested that this distribution might be due to the humidity requirements of the larvae. The purpose of the work discussed was to test this hypothesis.

The problem was investigated by measuring the relative humidities in nests by Solomon's method using cobalt chloride and cobalt thiocyanate papers, and by the artificial introduction of adult blackbird and hen fleas into the nests of the swallow and hole-nesting tits, in which the humidities were artificially modified. The experiments showed that the larvae of blackbird and hen fleas are able to survive in both dry and wet nests and that the larvae of the blackbird flea are greatly reduced in numbers or entirely eliminated when hen flea larvae are present in the nest.

Adult duck fleas were introduced into dry and wet nests of swallows. The results of the experiments showed that the larvae of the duck flea are able to survive in much drier nests than those of the flea's normal hosts.

It was suggested that the factor determining the difference in host selection between blackbird and hen fleas might be a difference in behaviour of the adults emerging from cocoons in the spring. Whenever the two species occur together in the same nest it is probable that the blackbird flea will eventually be eliminated. It was thought that the elimination of the blackbird flea was due to competition for food between the larvae and that the essential food substance might prove to be the blood faeces of the adult fleas.

Shortage of time prevented any lengthy discussions and it was pointed out that some data from nest boxes near Durham was available which gave rather different results for the distribution of the hen and blackbird fleas.

The President then thanked the speakers, and also gave the thanks of the Society to Professor Darlington and his Department for acting as hosts to the meeting.

R. ELFYN HUGHES

LIST OF MEMBERS (1 March 1956)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, C. H. Gimingham, Dept. of Botany, University of Aberdeen, Old Aberdeen.

E. Abeywickrama, B.A., B.SC., Dept. of Botany, University of Ceylon, Colombo, Ceylon.
E. A. Adams, L., A.B., M.S., California Forest and Range Experimental Station, Susanville, California, U.S.A.
E. Adamson, Prof. R. S., M.A., c/o Dept. of Botany, British Museum (Natural History), London, S.W.7.
E. Adcock, J. A., 50 Sandy Lane, Cooper Lane, Norwich, Norfolk.
E. Adlard, P. H., B.A., Dept of Forestry, P.O. Box 75, Limbe, Nyasaland.
A. Airey, A. F., M.B.O.U., Broadley's Cottage, Ghyll Head, Windermere, Westmorland.
A. Allee, Prof. W. C., 114 Leigh Hall, University of Florida, Gainsville, Florida, U.S.A.
A. Allen, E. F., B.A., M.B.O.U., Dept. of Agriculture, Kuala Lumpur, Perak, Malaya.
E. Allott, D. J., Fisons Ltd., Advisory Dept., Harvest House, Felixstowe, Suffolk.
E. Alston, A. H. G., M.A., Dept. of Botany, British Museum (Natural History), Cromwell Road, London, S.W.7.
E. Anderson, J. A. R., M.C., B.SC., State Forest Office, Brunei, Borneo.
E. Andrews, F. W., D.SC., PH.D., 172 Yardley Fields Road, Yardley, Birmingham, 25.
A. Arebrot-Olson, A., Stud. real; Gard pr., Haugesund, Norway.
E. Argyle, M. C., B.SC., A.C.F., P.O. Box 337, Forest Department, Nairobi, Kenya.
E. Armitage, Miss E., Foxdale, nr. Ross, Herefordshire (*Hon. Life Member*).
Ash, J. S., B.SC., M.B.O.U., I.C.I. Game Research Station, Burgate Manor, Fordingbridge, Hants. (*Associate Member*).
Ashby, K. R., B.A., Zoology Dept., The University, South Road, Durham (*Associate Member*).
E. Ashby, Dr M., Thorton House, Blundells Avenue, Tiverton, Devon.
E. Asprey, Prof. G. F., Dept. of Botany, University College, Newport Road, Cardiff.
E. A. Audy, J. R., M.B., B.SC., Institute for Medical Research, Kuala Lumpur, Malaya.
A. Auerbach, Dr S. I., 117 West Vanderbilt Drive, Oak Ridge, Tennessee, U.S.A.
E. Austwick, P. K. C., B.SC., Mycology Laboratory, Ministry of Agriculture and Fisheries Veterinary Laboratory, New Haw, nr. Weybridge, Surrey.
A. Badcock, Miss R. M., M.SC., Biological Dept., University College of N. Staffs., Keele, Staffs.
E. A. Bagenal, T., Marine Station, Keppel Pier, Millport, Isle of Cumbrae, Scotland.
E. A. Baker, H. G., PH.D., Botany Dept., University College of the Gold Coast, P.O. Box 4, Achimota, Gold Coast.
E. Bakker, Dr D., Biological Dept., Zuiderzee Reclamation Works, Baan 6, Ens (N.O. Polder), The Netherlands.
E. Balfour, Mrs E. J., Newton Hall, Kennoway, Windygates, Fife, Scotland.
A. Balfour-Browne, W. A. F., M.A., F.R.S.E., Brocklehirst, Collin, Dumfries, Scotland.
E. Ballantine, Miss D., B.SC., The Laboratory, Citadel Hill, Plymouth.
E. Ballantyne, A. O., B.SC., Department of Agriculture, P.O. Box 660, Lusaka, Northern Rhodesia.
E. Ballard, F., B.SC., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
E. Bally, P. R. O., Coryndon Memorial Museum, Nairobi, Kenya, E. Africa.
E. Balme, Miss O. E., M.SC., Cherry Trees, Rotherfield Greys, Henley-on-Thames, Oxon.
A. Band, R. M., 516 North Drive, Cleveleys, nr. Blackpool, Lancs.
E. A. Barker, J. A., F.Z.S., 27 Finchley Way, London, N.3.
A. Barker, T. W., B.SC., 346 Stones Villas, Walsdden, Todmorden, Lancs.

A. Barnes, H. F., ph.d., Rothamsted Experimental Station, Harpenden, Herts.
E. Barnes, Mrs M., m.sc., Lorne Villa, The Marine Parade, Millport, Isle of Cumbrae, Scotland.
E. A. Barrett, J. H., b.a., Dale Fort Field Centre, Haverfordwest, Pembrokeshire.
E. Barry, D. H., b.sc., Kumasi College of Technology, Private Bag, P.O. Kumasi, Gold Coast.
E. Bartley, D. D., b.sc., Botany Dept., University College of Wales, Aberystwyth.
E. Barton, Miss Frances M., 19 Park Street, Bath, Somerset.
E. A. Bassindale, R., m.sc., Zoology Dept., The University, Bristol.
A. Bates, J. K., Hope Dept. of Entomology, Oxford.
E. A. Bates, Dr Marston, Dept. of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. Bauchop, Isobyl F., b.sc., Tillycorthie Farm House, Udny Station, Aberdeen.
A. Baxter, Miss E. V., f.l.s., The Grove, Upper Largo, Fife, Scotland.
E. Bayer, Prof. A. W., d.sc., Dept. of Botany, Natal University College, Pietermaritzburg, S. Africa.
A. Beadle, Prof. L. C., m.a., Dept. of Zoology, Makerere University College, Kampala, Uganda.
E. Beard, Dr J., Natal Tanning Extract Co. Ltd., Pietermaritzburg, Natal, S. Africa.
E. Beddows, A. R., m.sc., Welsh Plant Breeding Station, Plas Gogerddan, nr. Aberystwyth.
E. A. Belcher, J. H., b.sc., 197 Risley Avenue, Tottenham, London, N.17.
E. Bell, Dr G. D. H., University School of Agriculture, Cambridge.
E. Bell, Prof. H. P., Botanical Laboratory, Dalhousie University, Halifax, Nova Scotia.
E. A. Bentley, Dr E. W., 41 Cumberland Road, Bromley, Kent.
A. Berg, Dr Kaj, Köbenhavns Universitets Forskvands, Biologiske Laboratorium, Hillerod, Denmark.
E. A. Bexon, Miss D., m.sc., University College, Nottingham.
E. Bhâradâwja, Prof. Y., m.sc., ph.d., Dept. of Botany, Banaras Hindu University, Banaras 5, India.
E. Bharucha, Prof. F. R., Institute of Science, Bombay 1, India.
E. A. Bingley, F. J., m.a., Flatford Mill Field Centre, East Bergholt, nr. Colchester, Essex.
A. Birch, L. C., m.sc., Zoology Dept., Columbia University, New York 27, U.S.A.
E. Birmingham Natural History and Philosophical Society, 114 Oxford Road, Moseley, Birmingham, 13 (C. E. A. Andrews, b.sc., f.l.s., *Hon. Treasurer*).
E. Birse, E. L., b.sc., Na Seileach, Woodburn Gardens, Aberdeen.
Birse, Mrs E. M., b.sc., Na Seileach, Woodburn Gardens, Aberdeen (*Associate Member*).
E. A. Blackburn, Miss K. B., d.sc., Botanical Dept., King's College, Newcastle-upon-Tyne 2.
A. Blackith, R. E., ph.d., b.sc., a.r.c.s., d.i.c., Imperial College Field Station, Sunninghill, Berkshire.
E. Blackman, Prof. G. E., Univ. Dept. of Agriculture, Oxford.
E. A. Blair, Gwendolyn Ann, b.sc., Hatton Court, Murtle, Milltimber, Aberdeenshire.
E. Blakelock, A., b.sc., f.l.s., The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
E. Blanchard, Miss B., b.sc., Hartley Botanical Laboratories, The University, Liverpool, 3.
E. Blank, T. H., b.sc., 'The Limes', Damerham, nr. Fordingbridge, Hants.
A. Bletchley, J. D., b.a., b.s.c., f.r.e.s., The Glebe Cottage, Little Kimble, nr. Aylesbury, Bucks.
E. Bloomer, H. H., 'Longdown', Sunnydale Road, Swanage, Dorset.
E. Boatman, D. J., b.sc., The Botany Dept., The University, Hull.
E. Böcher, Dr Tyge W., Universitetets Planteanatomiske Laboratorium, Gothersgade 140, Copenhagen K., Denmark.
E. Boeker, Dr Peter, Bonn, Katzenburgweg 5, Germany.

E. Bogdan, A. V., P.O. Box 338, Dept. of Agriculture, Nairobi, Kenya, British East Africa.
E. Boggie, R., 5 Seafield Avenue, Aberdeen, Scotland.
E. A. Bond, J. A., Dept. of Zoology, University of Chicago, Chicago 37, Illinois, U.S.A.
E. Boney, A. D., B.Sc., 24 Ford Park Road, Mutley, Plymouth.
A. Booth, A. H., Dept. of Zoology, University College of the Gold Coast, Achimota, Gold Coast.
E. Bor, N. L., C.I.E., M.A., D.Sc., F.L.S., Royal Botanic Gardens, Kew, Richmond, Surrey.
E. Boughey, Prof. A. S., Botany Dept., University College of Rhodesia and Nyas., 115 Baker Avenue, Salisbury, S. Rhodesia.
A. Bovey, Prof. P., Entomologisches Institut der Eidg. Tech. Hochschule, Universitätstrasse 2, Zürich, Switzerland.
E. Bowden, B. N., B.Sc., Samura Regional Research Station, Zaria, N. Nigeria, B.W.A.
E. A. Bowyer, F. H., M.B.E., Barclay Perkins & Co. Ltd., Park Street, Southwark, London, S.E.1.
A. Boyd, A. W., M.C., M.A., Frandley House, nr. Northwich, Cheshire.
E. Boyko, Dr H., Ministry of Agriculture, Ha' kirya, Tel-Aviv, Israel.
E. Bradshaw, A. D., B.A., Dept. of Agricultural Botany, University College of N. Wales, Bangor, N. Wales.
E. Bradshaw, Miss M. E., B.Sc., Dept. of Botany, University Science Laboratory, South Road, Durham.
E. Braid, Major K. W., M.A., B.Sc., Lochview, Skene, Aberdeenshire.
E. A. Brattstrom, Prof. Hans, Fil.Dr., Zoologisk Museum, Bergen, Norway.
E. Braun, Miss E. L., 5956 Salem Road, Cincinnati 30, Ohio, U.S.A.
E. Braun-Blanquet, Dr J., Station de Recherches Géobotaniques, Chemin du Pioch de Boutonnet, Montpellier, France.
E. Brett, D. W., 43 Penrhyn Avenue, Walthamstow, London, E.17.
E. Brett, Miss O. E., B.Sc., 13 The Vale, Woodford Green, Essex.
E. Brewer, Prof. H. E., Dept. of Botany, State College of Washington, Pullman, Washington, U.S.A.
E. A. Brian, M. V., M.A., Furzebrook Research Station, Wareham, Dorset.
E. Brierley, J. K., D.Phil., B.Sc., 162 Chorley New Road, Bolton, Lancs.
E. Bristol Naturalists' Society, Botanical Section, c/o Bristol Nat. Library, City Museum, Queens Road, Bristol.
A. Broadhead, E., M.A., B.Sc., D.Phil., Zoology Dept., The University, Leeds, Yorks.
E. A. Brockhouse, R. B., M.S., c/o Shell Oil Co., P.O. Box 1748, Baton Rouge, Louisiana, U.S.A.
E. A. Broembsen, H. H. v., B.Sc., 134 Verdoorn Street, Sunnyside, Pretoria, South Africa.
Brough, J. B., F.Z.S., M.B.O.U., 48 Greenleas Road, Wallasey, Cheshire (*Associate Member*).
A. Brown, A. G., M.R.C.S., L.R.C.P., Colac, Victoria, Australia.
A. Brown, E. S., B.A., Hailey Lodge, Hertford Heath, Hertford.
A. Brown, Miss F. M., 2 Osborne Road, Birkby, Huddersfield, Yorks.
E. A. Brown, H. D., B.Sc., Locust Research, Box 147, Middleburg, C.P., South Africa.
E. Brown, J. M. B., B.Sc., Forest Research Station, Alice Holt Lodge, Farnham, Surrey.
A. Brown, Mrs L. E., B.Sc., Ph.D., 4 Alwyne Road, Hanwell, London, W.7.
E. Brown, Miss Margaret E., Ph.D., 'Ken-Mar', 11 Royal Gardens, Boston Road, Hanwell, London, W.7.
A. Brown, V. M., B.Sc., 43 Kensington Gardens, Darlington, Durham.
Browning, T. O., Ph.D., Dept. of Zoology, University of Adelaide, Adelaide, Australia (*Associate Member*).
A. Brownlee, A., B.Sc., A.R.C. Field Station, Compton, nr. Newbury, Berks.
A. Bruce, Dr A. J., B.Sc., M.B., B.S., 49 Crown Road, Twickenham, Middlesex.
E. Brynard, A. M., M.Sc., Department of Botany, The University, Old Aberdeen.

E. Bullock, A. A., B.SC., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
A. Bullock, J. A., A.R.C.S., B.SC., F.R.E.S., Entomologist, P.O. Box 28, Nakuru, Kenya, E. Africa.
E. Bulman, Mrs M., Wentworth House, Chesterton Lane, Cambridge.
E. Bunting, B. T., B.A., 9 Aldam Road, Totley Rise, nr. Sheffield, Yorkshire.
E. Burbridge, Miss N. T., M.SC., Dept. of Plant Industry, C.S.I.R.O., P.O. Box 109, City, Canberra A.C.T., Australia.
E. A. Burckhardt, D., c/o Otto Josti, Zernez., Kt. Graubunden, Switzerland.
E. Burges, Prof. N. A., M.SC., PH.D., Hartley Botanical Labs., The University, Liverpool (*Vice-President*).
E. Burkill, I. H., M.A., 'Clova', The Mount, Leatherhead, Surrey.
E. Burman, H., A.R.I.C., A.M.I.CHEM.E., 'Crossburn', 48 Clock Road, Gawock, Renfrewshire, Scotland.
E. Burnett, Sir David H., BT., M.B.E., M.A., Tandridge Hall, nr. Oxted, Surrey.
E. A. Burnett, G. F., B.SC., D.I.C., P.O. Box 204, Arusha, Tanganyika, East Africa.
E. Burrows, Dr Elsie M., Hartley Botanical Laboratories, The University, Liverpool, 3.
E. Burton, Dr Marie B., 515 Tonbridge Road, Maidstone, Kent.
E. A. Burtt, B. L., B.SC., Royal Botanic Gardens, Edinburgh, 4.
A. Bush, Dr S. F., Dept. of Zoology, Natal University College, Pietermaritzburg, S. Africa.
E. Butcher, Dr R. W., B.SC., Cotherstone Cottage, Hillside Road, Burnham-on-Crouch, Essex.
E. A. Butler, F. H. C., M.A., M.SC., Ravensmead, Keston, Kent.
E. A. Buxton, Lt.-Col. E. N., B.A., M.C., Wallsgrove House, High Beach, Loughton, Essex.
E. Cadman, J. R., 1 Park View, Barony, Nantwich, Cheshire.
E. Caldwell, Prof. J., D.SC., PH.D., Dept. of Botany, University College of the South-West, Exeter.
E. Callens, Rev. Fr. Hubert, Jardin Gillet, Kisantu, Belgian Congo.
A. Campbell, B., PH.D. British Trust for Ornithology, 2 King Edward Street, Oxford.
E. Campbell, Miss M. S., F.L.S., Easter Tegarmucha by Aberfeldy, Perthshire.
E. A. Carpenter, K., 'Broad Gates', Bird Green, Beachamp Roding, Essex.
E. Carson, Dr G. P., 2 Chesterton Hall Crescent, Cambridge.
A. Carter, Dr G. S., Corpus Christi College, Cambridge.
E. A. Carter, J. E., M.A., 'Long Close', Prior Park Road, Ashby-de-la-Zouch, Leics.
E. Carter, Dr Nellie, 23 Mount Side, Guildford, Surrey.
E. Cartwright, J. B., B.SC., 50 Harris Street, Harris Park, N.S.W., Australia.
E. A. Castell, C. P., B.SC., Geological Dept., British Museum (Natural History), Cromwell Road. London, S.W.7.
E. Chadwick, N., M.SC., 37 Castle Road, Salisbury, Wilts.
E. Chalklin, Miss K. M., M.SC., Dept. of Botany, University Science Laboratories, South Road, Durham.
E. A. Chambers, Dr V. H., A.R.C.S., 47 Westbourne Road, Luton, Beds.
E. A. Champion, Prof. H. G., Imperial Forestry Institute, South Parks Road, Oxford.
A. Chandler, E. A., B.SC., Little Gate Rounds, Newdigate, Surrey.
A. Chant, D. A., B.A., M.A., F.A.O. Mission, Ministry of Agriculture, Baghdad, Iraq.
E. Chapman, Mrs E. M. H., c/o P.O.B. 179, Belleville, Ontario, Canada.
E. A. Chapman, K., M.A., B.SC., Keeper of Queen Victoria Museum, P.O. Box 6, Causeway, Salisbury, S. Rhodesia.
E. Chapman, P. C., Charterhouse School, Godalming, Surrey.
E. Chapman, Prof. V. J., B.A., PH.D., Dept. of Botany, University College, Auckland, New Zealand.
E. Chapple, J. F. G., F.L.S., The Brackens, Nicholas Way, Northwood, Middlesex.
E. Chater, E. H., M.SC., Windover, Aberystwyth, Wales.
E. Chatto, A. E., White Barn Farm, Elmstead, Colchester, Essex.
E. A. Chear, John, F.L.S., 17 Elmwood, Welwyn Garden City, Herts.

E. A. Chew, R. M., ph.d., Dept. of Zoology, University of Southern California, 3518 University Avenue, Los Angeles 7, California, U.S.A.
A. Chitty, D. H., Bureau of Animal Population, Botanic Garden, High Street, Oxford.
E. Christie, M. G., b.a., E.A. Malaria Unit, P.O. Amani, Tanga, Tanganyika, E. Africa.
E. Clapham, Prof. A. R., Botanical Dept., The University, Sheffield 10, Yorks.
E. Clark, W. A., ph.d., Dept. of Botany, King's College, Newcastle-upon-Tyne, 2.
E. Clayton, W. D., b.sc., E.E.A. and F.R.O., Box 21, Kikuyu, Kenya, Brit. East Africa.
E. Clifford, H. T., m.sc.(melb.), University College, Ibadan, Nigeria.
A. Cloudsley-Thompson, Hon. Capt. J. L., m.a., ph.d., f.l.s., Glendoone, 10 Lower Green Road, Esher, Surrey.
E. Clowes, Dr F. A. L., Dept. of Botany, South Parks Road, Oxford.
A. Colquhoun, M. K., Common Farm, Blackthorn, Bicester, Oxon.
E. A. Conder, P. J., 5 Bedales, Scaynes Hill, nr. Hayward's Heath, Sussex.
A. Condry, W. M., m.a., Felin y Cwm, Egwysfach, Machynlleth, Mont.
E. A. Connell, J. H., b.s., m.a., Dept. of Biological Sciences, Santa Barbara College, University of California, Goleta, California, U.S.A.
E. Conolly, Miss A. P., m.a., Botany Dept., University College, Leicester.
E. A. Conway, H. T., b.sc., Dept. of Education, University College of Wales, 9 Marine Terrace, Aberystwyth.
E. Conway, Mrs E., Botany Dept., The University, Glasgow, W.2.
E. Conway, Miss V. M., ph.d., The Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.
E. Coombe, D. E., m.a., ph.d., Botany School, Downing Street, Cambridge.
E. A. Coombs, Charles W., m.sc., d.s.i.r., Pest Infestation Laboratory, London Road, Slough, Bucks.
E. Cooper, J. P., b.sc., Welsh Pl. Breed. Sta., Plas Gogerddan, nr. Aberystwyth.
E. Cooper, Prof. W. S., 1421 Bluebell Avenue, Boulder, Colorado, U.S.A.
A. Corbet, P. S., b.sc., f.r.e.s., Dept. of Zoology, Downing Street, Cambridge.
A. Corlett, J., m.sc., Fisheries Laboratory, Lowestoft, Suffolk.
E. Cornish, Miss M. W., b.sc., m.sc., 10 Northampton Lane, Croydon, Surrey.
E. A. Coulson, B. W. H., The School, Oundle, nr. Peterborough.
A. Coulson, J. C., b.sc., Dept. of Zoology, South Road, Durham City.
E. Coupland, R. T., ph.d., Dept. of Plant Ecology, University of Saskatchewan, Saskatoon, Canada.
E. A. Cragg, Prof. J. B., m.sc., Dept. of Zoology, Science Laboratories, South Road, Durham.
E. Creber, G. T., b.sc., 'Applecroft', Meadowcot Lane, Coleshill, Amersham, Bucks.
E. Crespin, J. F., b.a., The School, Dartington Hall, S. Devon.
E. Crisp, Dr D. J., Marine Biology Station, University College of North Wales, Menai Bridge, Anglesey.
E. Crocker, Prof. R. L., d.sc., Dept. of Botany, The University, Sydney, Australia.
E. Croker, Miss B. H., m.sc., 103 Upland Road, Wellington, W.1, New Zealand.
E. Crowder, Mrs A. A., b.a., Flat 3, 19 Chlorine Gardens, Belfast, N. Ireland.
E. Croydon Natural History and Scientific Society, c/o B. R. H. Tombleson, Esq., o.b.e. (*Hon. Gen. Sec.*), 41 Bigginwood Road, Norbury, London, S.W.16.
E. Crundwell, A. C., Dept. of Botany, The University, Glasgow, W.2.
E. Curtis, Prof. J. T., Botany Dept., Biology Building, University of Wisconsin, Madison 6, Wis., U.S.A.
E. Curtis, Miss W. M., ph.d., Botany Dept., University of Tasmania, Hobart, Tasmania.
A. Curry-Lindahl, K., Zoological Dept., Nordiska Museet, Stockholm, Sweden.
E. Daggash, M., c/o Forest Dept., Katsina, N. Nigeria.
E. Dalby, D. H., b.sc., 108 Gordon Road, Camberley, Surrey.
A. Dalgety, C. T., Lockerley Hall, Romsey, Hants.
E. A. Dansereau, Dr P., Institut Botanique de l'Université de Montreal, 4101 est, rue Sherbrooke, Montreal, 36, Canada.

E. A. Darling, F. F., D.Sc., Ph.D., F.R.S.E., Shefford, Woodlands House, Newbury, Berks.
E. Davenport, Miss E., B.Sc., 3 Sheldon Avenue, Vicars Cross, Chester.
E. Davey, Miss A. J., M.Sc., 20 Deiniol Road, Bangor, N. Wales.
E. Davies, Miss E. W., B.Sc., Botany Dept., The University, Leeds.
E. A. Davies, J. Ll., M.A., Geography Dept., University of Tasmania, Hobart, Tasmania.
A. Davies, L., Ph.D., Dept. of Zoology, University Science Laboratories, South Road, Durham.
Davies, O. J. H., Barbers Orchard, Little Baddow, Essex (*Associate Member*).
E. Davies, Dr Wm., 'Whitegables', Shiplake-on-Thames, Oxon.
E. Davis, Prof. A. G., B.S.A., M.Sc., Dept. of Agriculture, University College of Rhodesia and Nyas., 115 Baker Avenue, Salisbury, S. Rhodesia.
E. A. Davis, D. H. S., Plague Research Laboratory, P.O. Box 1038, Johannesburg, S. Africa.
E. Davis, P. H., B.Sc., F.L.S., Dept. of Botany, Royal Botanic Gardens, Edinburgh, 4.
E. A. Davis, T. A. W., South Mulloch, Haverfordwest, Pembrokeshire.
A. Davis, W. B., Ph.D., Box 254 FE, College Station, Texas, U.S.A.
E. Dawkins, H. C., M.A., c/o Forest Dept., Entebbe, Uganda, E. Africa.
A. Day, Dr J. H., Dept. of Zoology, University of Cape Town, S. Africa.
A. Delany, M. J., B.Sc., Dept. of Zoology, The University, Southampton.
A. Dempster, J. P., Ph.D., D.I.C., 6 Southcote Road, Tufnell Park, London, N.19.
E. De Rousset-Hall, O., M.A., 44 Great Bowden Road, Market Harborough, Leics.
A. De Rousset-Hall, Mrs P. J., 44 Great Bowden Road, Market Harborough, Leics.
A. DeWitt, R. M., Ph.D., Biology Dept., University of Florida, Gainesville, Florida, U.S.A.
E. A. Dice, Lee R., Ph.D., Institute of Human Biology, 1135 E. Catherine Street, Ann Arbor, Michigan, U.S.A.
E. Dick, Michael W., 5 Fairway, West Wimbledon, London, S.W.20.
E. A. Digby, Peter S. B., Dept. of Biology, St. Thomas's Hospital Medical School, London, S.E.1.
E. Dilnot, Miss J., B.Sc., School of Agriculture, Sutton Bonnington, Loughborough.
E. Dimbleby, G. W., M.A., D.Phil., Imperial Forestry Institute, South Parks Road, Oxford.
E. A. Diver, Capt. C., C.B.E., Rushmere Cottage, Frensham, Surrey (*Vice-President*).
A. Dixon, A. F. G., Hope Dept. of Entomology, University Museum, Oxford.
E. Dony, J. G., Ph.D., 41 Somerset Avenue, Luton, Beds.
E. Donnelly, Joseph, B.Sc., Field Research Laboratory, Blackford, Carlisle.
E. Douglas, Miss Barbara, B.Sc., Ferry House, Far Sawrey, Ambleside, Westmorland.
E. A. Dowdeswell, W. H., M.A., 5 Kingsgate Street, Winchester, Hants.
A. Driver, P. M., Warnless Cottage, Bond End, Upton St. Leonards, Gloucester.
E. A. Drummond, R. B., B.Sc., The Branch of Botany and Plant Pathology, Dept. of Research, P.O. Box 8100, Causeway, Salisbury, S. Rhodesia.
A. Duffey, E. A. G., B.Sc., 400 Dercham Road, Norwich.
A. Duncan, Miss A., B.Sc., Royal Holloway College, Englefield Green, Surrey.
A. Duncan, A. B., B.A., Gilchrist and Closeburn, Thornhill, Dumfries, Scotland.
A. Dunnett, G. M., B.Sc., C.S.I.R.O., Wildlife Survey Section, P.O. Box 109, City, Canberra, A.C.T., Australia.
E. Du Rietz, Prof. Einar, Växtbiologiska Institutionen, Uppsala, Sweden.
E. Durno, S. E., B.Sc., Macaulay Institute for Soil Research, Craigiebuckler, Aberdeen, Scotland.
E. A. Dussart, B. H., D.E.S., Station de Recherches Lacustres de Thonon (Haute Savoie), France.
A. Edelstam, Carl G., Östermalmsgatan 61, Stockholm 5, Sweden.
A. Edinburgh University Biological Society, Royal Botanic Gardens, Edinburgh.
A. Edwards, R. L., M.A., D.Phil., Dept. of Zoology, The University, Hull, E. Yorks.
E. Eggeling, W. J., B.Sc., Ph.D., Brockness House, Ladywalk, Anstruther, Fife, Scotland.
E. Elder, N. L., M.A., F.R.G.S., 43 McHardy Street, Havelock North, New Zealand.

E. Eliott, R. J., M.C., B.SC., PH.D., The Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.
E. A. Elton, Charles, Bureau of Animal Population, Dept. of Zoological Field Studies, Botanic Garden, High Street, Oxford.
A. El-Ziady, Miss Samira A. E., B.SC., M.SC., Dept. of Entomology, University of Cairo, Giza, Egypt.
E. England, F. J. W., B.SC., c/o Scottish Plant Breeding Station, Pentlandfield, Roslin, Midlothian.
E. Essex Field Club, The, Essex Museum of Natural History, Romford Road, Stratford, London, E.15.
E. Evans, Miss E. M., B.SC., PH.D., Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.
E. Evans, E. Price, 6 Barrowfield Drive, Hove 4, Brighton, Sussex.
E. A. Evans, F. C., Institute of Human Biology, University of Michigan, 1135 E. Catherine Street, Ann Arbor, Michigan, U.S.A.
E. Evans, Dr G. C., Botany School, Downing Street, Cambridge.
A. Evans, Dr Gwilym O., British Museum (Natural History), Cromwell Road, London, S.W.7.
A. Fager, E. W., B.A.(YALE), PH.D.(YALE), c/o Scripps Institute of Oceanography, La Jolla, California, U.S.A.
E. Falk, P., Tudor House, Horton Crescent, Rugby.
E. Fanshawe, D. B., B.A., Forest Dept., P.O. Box 228, Ndola, N. Rhodesia.
A. Fauchald, K., Jr., stud. real., Kirkegt 6, Kristiansand S., Bergen, Norway.
E. Fenton, E. Wyllie, D.SC., 'Knowehead', Milltimber, Aberdeenshire.
A. Fenton, G. R., B.A., B.SC., Church Farm, Gringley on the Hill, nr. Doncaster, Yorks.
E. A. Fernando, C. H., B.SC., (Ceylon) Hope Dept. of Entomology, Oxford.
E. Ferreira, R. E. C., B.SC., Dept. of Botany, University of Aberdeen, Old Aberdeen.
A. Fidler, Dr J. H., Ministry of Agriculture and Fisheries, University College of S. Wales and Mon., Cathays Park, Cardiff.
E. A. Fincher, F., Randan Wood, Woodcote, Bromsgrove, Worcs.
E. A. Fisher, James M. McC., M.A., Old Rectory, Ashton, Northampton.
A. Fitter, R. S. R., B.SC.(ECON.), Drifts, Chinnor Hill, Oxford.
A. FitzPatrick, Mrs M. J., 8 Cumberland Road, Barnes, London, S.W.13.
E. Fleming, Dr G. W. T. H., F.L.S., Barnwood House, Gloucester.
E. Foggie, A., B.SC., c/o Chief Conservator of Forests, P.O. Box 527, Accra, Gold Coast.
A. Ford, J., Tsetse Research Dept., Shinyanga, Tanganyika Territory, E. Africa.
E. A. Forster, G. R., B.SC., Marine Biological Laboratory, Citadel Hill, Plymouth.
Fountain, Rev. A. F., M.SC., Dale Vicarage, Haverfordwest,Pembrokeshire.
E. Fourt, D. F., c/o Forest Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey.
E. Frank, Dr Erica M., Box 31, Oak Glen Station, Lansing, Ill., U.S.A.
E. Fraser, D. A., B.A., Petawawa Forest Experiment Station, Chalk River, Ontario, Canada.
A. Freeman, Dr J. A., Ministry of Agriculture and Fisheries, Infestation Control Division, Hook Rise, Tolworth, Surbiton, Surrey.
A. French, R. A., B.SC., Rothamsted Experimental Station, Harpenden, Herts.
A. Frings, Prof. Hubert W., PH.D., Dept. of Zoology, The Pennsylvania State University, University Park, Pennsylvania, U.S.A.
E. Frost, L. C., B.A., Albion Lodge, 4A Cotman Road, Norwich, Norfolk.
E. Frost, Miss L. W., B.SC., 98 Bolton Road, Salford 6, Lancs.
A. Frost, Miss W. E., The Ferry House, Far Sawrey, Ambleside, Westmorland.
A. Froud, M. D., B.SC., The College, Wye, Ashford, Kent.
E. Fulford, R. M., Pomology Dept., East Malling Research Station, East Malling, Maidstone, Kent.
A. Gabbutt, P. D., B.SC., 44 Wayside Avenue, Harrogate, Yorks.
E. Galt, R. W. C., B.SC., 20 Braid Farm Road, Edinburgh.
E. Gams, Dr Helmut, Schneeburggasse 67, Innsbruck-Hötting, Austria.

E. GARDNER, Dr G., School of Higher Commercial Studies, 535 Viger Avenue, Montreal, Canada.
E. GATES, L. F., B.A., Dunholme Field Station, Dunholme Holt, Lincoln.
A. GAULD, D. T., PH.D., Dept. of Zoology, University College of the Gold Coast, Achimota, Gold Coast, W. Africa.
E. GAY, P. A., B.SC., School House, Hartbury, Glos.
E. A. GENSCH, R. H., 105 Clark Avenue, Billings, Montana, U.S.A.
E. GERMAIN, Dr R., Institut National pour l'Étude Agronomique du Congo Belge, Yangambi, Congo Belge.
E. GIBBY, Mrs A. N., B.SC., A.R.I.C., Prebend's Gate, Quarry Heads Lane, Durham.
E. GIBSON, Miss C. M., 'Trematon', 11 South Leigh Road, Havant, Hants.
A. GILBERT, N., 12 Harcourt Road, Bristol 6.
A. GILBERT, O. J. W., M.SC., B.SC., The Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.
E. GILBERT-CARTER, H., M.A., M.B., 'Thatches', Holcombe, Dawlish, Devon.
E. A. GILLETT, J. B., M.A., 40 Pensford Avenue, Richmond, Surrey.
E. GILLHAM, Miss M. E., B.SC., PH.D., Dept. of Botany, University College of the South-West, Exeter.
E. GILLILAND, Prof. H. B., Dept. of Botany, University of Malaya, Singapore, Malaya.
E. GILLMAN, H., M.SC., 151 Oakwood Court, London, W.14.
E. GILMOUR, J. S. L., M.A., Director, University Botanic Garden, Cory Lodge, Hills Road, Cambridge.
E. GILSON, Mrs M. R., PH.D., Sawrey House, Near Sawrey, Ambleside, Westmorland.
A. GILSON, H. C., The Ferry House, Far Sawrey, Ambleside, Westmorland (*Hon. Editor of Journal of Animal Ecology*).
E. GIMINGHAM, C. H., B.A., PH.D., Dept. of Botany, University of Aberdeen, Old Aberdeen (*Hon. Secretary*).
E. GLAISTER, Mrs K., 12 Grey Close, London, N.W.11.
E. A. GLASGOW AND ANDERSONIAN NAT. HIST. AND MICROSCOPICAL SOC., Societies' Rooms, Royal Technical College, Glasgow, C.1.
A. GLASGOW, Dr J. P., EATTRRO, Shinyanga, Tanganyika, E. Africa.
E. GLEDHILL, Mrs E. E. A., M.SC., 20 C African Street, Grahamstown, S. Africa.
E. A. GLOVER, Major P. E., M.SC., c/o EATTRRO, P.O. Box 2141, Nairobi, Kenya.
A. GODFREY, Miss G. K., 117 Waldegrave Road, Teddington, Middlesex.
E. GODWARD, Dr Maud, B.E., 8 Deyncourt Gardens, Upminster, Essex.
E. A. GODWIN, H., SC.D., F.R.S., Botany School, Cambridge (*Hon. Editor, Journal of Ecology*).
E. A. GOOD, Prof. R. D'O., M.A., SC.D., Botanical Dept., University College, Hull.
E. GOODALL, D. W., D.SC., PH.D., D.I.C., Dept. of Agricultural Botany, The University, Reading, Berks.
A. GOODBODY, I. M., B.A., University College of the West Indies, Mona, St. Andrews, Jamaica, B.W.I.
A. GOODHART, C. B., Museum of Zoology, Downing Street, Cambridge.
E. A. GOODIER, R., B.SC., Tsetse Fly Operations Dept., P.O. Box. 8100, Causeway, Salisbury, S. Rhodesia.
E. GOODMAN, G. T., B.SC., Dept. of Botany, University College of Swansea, Singleton Park, Swansea, Glamorgan.
E. GOODWAY, K. M., B.A., The Dept. of Biology, University of North Staffordshire, Keele, Staffs.
E. GOODWIN, Du Wayne, L., M.S., PH.D., Dept. of Range Management, School of Forest, Range and Wild Life Management, Utah State Agricultural College, Logan, Utah, U.S.A.
A. GOONEWARDENE, T. P., B.SC.(LOND.) Fisheries Research Station, P.O. Box 531, Columbo, Ceylon.
E. GORE, A. J. P., B.SC., Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancashire.
E. GORHAM, Eville, M.SC., Freshwater Biological Association, Ferry House, Far Sawrey, Ambleside, Westmorland.

A. GRADWELL, G. R., M.A., Hope Dept. of Entomology, University Museum, Oxford.
E. GREEN, P. S., B.SC., Royal Botanic Garden, Edinburgh, 4.
E. A. GREENLEES, G. I. L., Dinwoodie, Hollybush, by Ayr, Scotland.
A. GREENSLADE, P. J. M., Machon Bank, Maryfield Avenue, Exeter.
E. GREENWAY, P. J., F.L.S., East African Herbarium, P.O. Box 5166, Nairobi, Kenya Colony.
E. GREIG-SMITH, P., B.A., Dept. of Botany, University College of North Wales, Bangor
E. GROSE, J. D., Downs Edge, Liddington, nr. Swindon, Wilts.
E. GROVE, A. T., M.A., Dept. of Geography, Downing Place, Cambridge.
A. GUDJONSSON, T. V., M.SC., P.O. Box 754, Reykjavik, Iceland.
E. A. GUDMUNDSSON, Dr F., Náttúrugripasafnid, P.O. Box 532, Reykjavik, Iceland.
E. A. HAARLØV, N., M.SC., Royal Veterinary and Agricultural College, Zoological Laboratory, Bulowsvej 13, Copenhagen V, Denmark.
E. A. HADDOW, Dr A. J., M.B., CH.B., B.SC., D.P.M. and H., Yellow Fever Research Institute, Field Box 49, Entebbe, Uganda, E. Africa.
A. HAIRSTON, N. G., M.A., PH.D., Dept. of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. HALKET, Miss A. C., D.SC., 'Tupra', Elstead, nr. Godalming, Surrey.
E. HALL, I. V., PH.D., Botany and Plant Pathology Division, Laboratory of Plant Pathology, Kentville, N.S., Canada.
A. HALL, R. E., A.R.C.S., B.SC., Dept. of Zoology, The University, Southampton.
E. HALL, R. H., 2 Hartington Terrace, West Road, Buxton, Derbyshire.
A. HALLGRIMSSON, I., mag. Scient., Fiskideild, Borgartun 7, Reykjavik, Iceland.
E. EL-HALWAGY, R., B.SC., Dept. of Botany, Faculty of Science, University of Alexandria, Egypt.
E. HAMBLER, D. J., B.SC., 146 Lancelot Avenue, Strood, Rochester, Kent.
A. HAMERSTROM, Dr F., Plainfield, Wisconsin, U.S.A.
A. HAMILTON, J. D., B.SC., Zoology Dept., The University, Glasgow, W.2.
E. HAMILTON, Miss M. N., B.SC., 7 Beechwood Avenue, Londonderry, N. Ireland.
E. HARBERD, D. J., M.SC., Scottish Soc. for Research in Plant Breeding, Pentlandfield, Roslin, Midlothian.
A. HARDY, Prof. A. C., M.A., D.SC., F.R.S., University Dept. of Zoology, Oxford.
E. HARLEY, J. L., M.A., D.PHIL., University Dept. of Botany, South Parks Road, Oxford.
E. HARPER, J. L., B.SC., University Dept. of Agriculture, Parks Road, Oxford.
E. HARPER, P. C., B.SC., Edinburgh and E. of Scotland College of Agriculture, 13 George Square, Edinburgh, 9.
A. HARRIS, L. F., The Arcade Bookshop, 24 The Arcade, Long Wyre Street, Colchester, Essex.
A. HARRIS, Prof. T. M., M.A., SC.D., F.R.S., Botany Dept., The University, Reading, Berks.
A. HARRISON, A. D., M.SC., C.S.I.R., Water Res. Div., Hut T, 10 Witwatersrand University, Johannesburg, South Africa.
A. HARTLAND-ROWE, R. C. B., B.SC., Dept. of Biology, Makerere College, P.O. Box 262, Kampala, Uganda, E. Africa.
A. HARTLEY, Rev. P. H. T., B.SC., Badingham Rectory, nr. Woodbridge, Suffolk.
E. A. HARVEY, Prof. L. A., M.SC., Dept. of Zoology, University of Exeter, Exeter. Devon.
E. HAYNES, F. N., B.SC., Botany Dept., The University, Sheffield.
E. HAYWOOD, J., B.SC., 6 Pendre, Bridgend, Glamorgan.
E. HEDDLE, R. G., M.A., B.SC., Edinburgh and E. of Scotland College of Agriculture, 13 George Square, Edinburgh.
E. A. HEMMING, C. E., B.A., Desert Locust Survey, P.O. Box 5152, Nairobi, Kenya, British E. Africa.
E. HEMSLEY, J. H., B.SC., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
A. HENDERSON, Miss M., 44 Higher Bebington Road, Bebington, Cheshire.
E. A. HEPBURN, I., M.A., 18 South Road, Oundle, Peterborough.

E. Hepper, F. N. B.SC., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
E. A. Heslop-Harrison, J. Prof., M.SC., PH.D., Botany Dept., University College, Gower Street, London, W.C.1.
E. A. Heslop-Harrison, Prof. J. W., F.R.S., Dept. of Botany, Queen's University, Belfast, Northern Ireland.
A. Hewer, H. R., A.R.C.S., M.SC., Dept. of Zoology and Applied Entomology, Imperial College, London, S.W.7.
E. Hewetson, C. E., 27 Crestway, Roehampton, London, S. W. 15.
E. Hewitt, Miss M. S., 92 Park Avenue, Kingston-upon-Hull, Yorks.
E. Heywood, V. H., PH.D., F.L.S., B.SC., The Hartley Botanical Lab., The University, Liverpool, 3.
E. Hilton, J. R., B.SC., Greycott, Golant, Par, Cornwall.
E. A. Hinchcliffe, R., B.A., Belmont Station, Box 455, Broken Hill, N.S.W., Australia.
E. A. Hindle, G. B., B.SC., King's Norton Grammar School for Boys, Birmingham, 30.
A. Hobart, J., B.SC., Dept. of Agricultural Zoology, University College, Bangor, North Wales.
A. Hobby, B. M., M.A., D.PHIL., Hope Dept., University Museum, Parks Road, Oxford
E. Hodge, C. A. H., B.SC., Rothamsted Experimental Station, Harpenden, Herts.
A. Hodgkin, E. P., 6 Princes Street, Mosman Park, Western Australia.
A. Hoestlandt, Professor L'Abbé H., D.SC., Faculté libre des Sciences, 13 rue de Toul, Lille (Nord), France.
E. A. Hoffman, L., Tour du Valat, par le Sambuc, B. d. Rh., France.
A. Holden, M. J., B.A., West African Fisheries Research Institute, Field Station, Birnin Kebbi, Sokoto Province, Nigeria.
E. Holdgate, M. W., B.A., Queen's College, Cambridge.
E. Hole, Miss D. R., B.SC., Rousdon, Cutbush Lane, Shinfield, Reading, Berks.
A. Holme, N. A., B.A., The Laboratory, Citadel Hill, Plymouth.
E. A. Holmes, P. F., M.A., Malham Tarn Field Centre, nr. Settle, Yorks.
A. Holt, S. J., B.SC., 35 Sheaveshill Avenue, Colindale, London, N.W.9.
E. Holttum, Prof. R. E., M.A., 80 Mortlake Road, Kew Gardens, Richmond, Surrey.
E. A. Holway, P. H., B.A., Colfe's Grammar School, Lewisham, London, S.E.13.
E. Hooper, M. D., 7 Essex Road, London, E.4.
E. Hope-Simpson, J. F., D.PHIL., Dept. of Botany, The University, Bristol, 8.
E. Hopkins, B., B.SC., Botany Dept., University College, Ibadan, Nigeria.
A. Hori, J. N., A.M.I.E.E., 'Heathcroft', Poplar Close, New Barn, Longfield, Kent.
E. A. Hornby, H. E., F.R.C.V.S., Poole Farm, Hartley, S. Rhodesia.
E. Horne, F. R., M.A., Hill Farm, Lolworth, Cambs.
A. Horridge, G. A., B.A., St. John's College, Cambridge.
E. Hoyle, A. C., M.A., 2 Templar Road, Oxford.
E. Hubbard, C. E., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey (*Hon. Treasurer*, receives subscriptions).
A. Huddart, B. J., Shirley House, Marsh Lane, Taplow, Bucks.
E. Hughes, A. P., B.A., The Botany School, Cambridge.
E. Hughes, F. E., B.A., c/o Westminster Bank, High Street, Oxford.
E. Hughes, R. Elfyn, M.A., PH.D., Nature Conservancy, School of Agriculture, U.C.N.W., Memorial Buildings, Bangor, N. Wales.
A. Hume, Major C. W., 284 Regent's Park Road, Finchley, London, N.3.
E. Hunt, P. F., 19 Victoria Road, Frome, Somerset.
E. A. Huxley, T., Balliol College, Oxford.
E. Hyde, H. A., M.A., Dept. of Botany, National Museum of Wales, Cardiff, S. Wales.
A. Hyde-Wyatt, B., B.SC., A.R.C.S., F.R.E.S., Dept. of Tsetse Fly Control, W.A., Northern Territory, Gold Coast.
A. Hynes, H. B., PH.D., Dept. of Zoology, The University, Liverpool.
A. Ibbotson, Alan, D.I.C., DIP.AG.SCI.(CANTAB.), F.R.E.S., University School of Agriculture, The Quadrangle, King's College, Newcastle-upon-Tyne, 1.
A. Ingle, R. W., Zoology Dept., British Museum (Natural History), London, S.W.7.
E. Irvine, F. R., D.SC., 32 Tavistock Square, London, W.C.1.

E. Irvine, Mrs L. M., B.SC., 21 Cranmer Road, Cambridge.
E. Ivens, G. W., C.I.R.U., P.O. Box 204, Arusha, Tanganyika, E. Africa.
E. Ivimey-Cook, R. B., B.SC., Galmington, Radyr, Cardiff, Glamorgan.
E. Jackson, A. C., B.SC., 37 Lynton Avenue, Chanterlands Avenue, Hull, Yorks.
E. A. Jackson, D. S., B.A., P.O. Puketapu, Hawkes Bay, New Zealand.
E. Jackson, G., B.SC., 4 Rivelin Park Road, Sheffield, 6, Yorks.
E. Jackson, J. K., B.SC., Forestry Officer, F.A.O., c/o Forest Office, Arbil, Iraq.
E. Jackson, R. M., B.SC., Division of Agriculture, Botany, Faculty of Agriculture, University College, Ibadan, Nigeria.
A. Jacob, F. H., M.SC., Plant Pathology Laboratory, Milton Road, Harpenden, Herts.
A. Jameson, E. W., Jr., B.S., M.A., Division of Zoology, University of California, Davis, California, U.S.A.
E. Jameson, J. H., M.A., 25 Radnor Road, Handsworth, Birmingham, 20.
E. Jane, Prof. F. W., D.SC., F.L.S., Highfield, Egham Hill, Englefield Green, Surrey.
E. Jaques, Miss M., 'Egmont', St. James Lane, Winchester, Hants.
E. A. Jarrett, T., Tsetse Survey and Control, Dept. of Veterinary Service, c/o Veterinary Laboratory, Kabete, Kenya Colony.
A. Jary, S. G., South-Eastern Agricultural College, Wye, Ashford, Kent.
Jennings, O. E., Carnegie Museum, Pittsburg, Pa., U.S.A. (*Hon. Life Member*).
E. Jermy, A. C., 'Tandem', East Avenue, Brundall, nr. Norwich, Norfolk.
A. Johansson, A. S., Zoological Laboratory, University of Oslo, Blindern, Norway.
E. Johnson, C. S. E., B.A., Norwi Farm, Private Bag 31, Concession, Southern Rhodesia.
A. Johnson, D. S., B.A., Dept. of Zoology, Bedford College, London, N.W.1.
E. A. Johnson, F. M., A.M.I.MECH.E., A.M.I.M.I., 22 Bellevue Crescent, Duffield, nr. Derby.
A. Johnson, J. H., 1 Berry Street, Hepthorne Lane, Chesterfield.
Johnson, Thomas J., F.C.I., F.S.C., etc., 'Wyddrington', Hugh Road, Smethwick, Staffs.
A. Jonasson, P. M., M.SC., Adolf Steens Alle 4II, Copenhagen, N. Denmark.
E. Jones, Dr E. W., Imperial Forestry Institute, South Parks Road, Oxford.
E. Jones, F. R., 139 Halfway Street, Sidcup, Kent.
E. Jones, Miss G. M., The Cottage, Wraysbury, Bucks.
E. Jones, H., M.SC., PH.D., Dept. of Botany, University College of Wales, Aberystwyth, Wales.
E. Jones, H. M., B.SC.(WALES), 92 Penrhiwceiber Road, Penrhiwceiber, Mountain Ash, Glamorganshire.
A. Jones, N. S., M.SC., Marine Biological Station, Port Erin, Isle of Man.
A. Jones, R. J., B.A., Whitgift School, Haling Park, South Croydon, Surrey.
E. Jones, Mrs V., B.SC., The Nature Conservancy, c/o School of Agriculture, University College of North Wales, Bangor.
A. Jordan, A. M., B.SC., The West African Inst. for Trypanosomiasis Research, Kaduna, N. Nigeria.
E. Joshi, M. C., M.SC., Asst. Professor of Botany; Botany Dept., Bisla College of Science, P.O., Pilani (Rajasthan), India.
E. Jowsey, P. C., B.SC., Leasingside Cottage, Balerno, Midlothian.
E. Kamel, Dr Mostafa, Faculty of Agriculture, Cairo University, Giza, Egypt.
E. Kassas, M. A. F. El-, M.SC., PH.D., Faculty of Science, University of Cairo, Giza, Egypt.
E. Keay, R. W. J., M.A., F.L.S., 40 Fairfax Road, Teddington, Middlesex.
A. Kellen, A. K. I., B.SC., 4 St. Anne's Place, Hakin, Milford Haven, Pembrokeshire.
A. Kendeigh, S. C., PH.D., Vivarium Building, University of Illinois, Wright and Healey Streets, Champaign, Illinois, U.S.A.
E. Kershaw, K. A., B.SC., Blackwall Cottage, Kirk Ireton, Derbyshire.
A. Kettle, D. S., M.SC., Dept. of Zoology, West Mains Road, Edinburgh, 9.
E. King, J. B.SC., PH.D., Hill Farming Research Organization, Sourhope Farm, Yetholm, Kelso, Roxburghshire.
A. King, J. A., Roscoe B. Jackson Memorial Laboratory, P.O. Box 847, Bar Harbor, Maine, U.S.A.

E. Kipling, T. H., B.A., 161 Main Road, Duston, Northampton.
A. Kitching, J. A., M.A., Zoology Dept., The University, Bristol, 8.
E. Klika, Prof. Jaromír, PH.D., École polytechnique, Praha—Kosire 333, Czechoslovakia.
A. Klopman, R. B., 13 Timberline Road, Hohokus, New Jersey, U.S.A.
E. Knight, G., 39 High Street, Northwood, Middlesex.
A. Knight-Jones, E. W., B.SC., D.PHIL., Marine Biological Station, Bangor, N. Wales
E. A. Knox, G. A., B.A., M.SC., Zoology Dept., Canterbury University College, Christchurch, New Zealand.
E. de Kock, Dr P. C., M.SC., D.PHIL., Macaulay Institute for Soil Research, Craigiebuckler, Aberdeen.
A. Kristensen, Dr I., Zoological Station, Buitenhaven, Den Helder, Holland.
A. Krumholz, L. A., PH.D., c/o Lerner Marine Laboratory, Bimini, Bahamas, British West Indies.
A. Lack, D., SC.D., Edward Grey Inst. of Field Ornithology, Dept. of Zoological Field Studies, Botanic Garden, High Street, Oxford.
E. A. Laing, C. C., PH.D., Dept. of Botany, Engineering Building, University of Wyoming, Laramie, Wyo., U.S.A.
E. Lambert, Miss J. M., PH.D., Dept. of Botany, The University, Southampton.
E. Landon, F. H., Forest Research Station, Kepong, Malaya.
E. Langdale-Brown, I., P.O. Box 265, Kampala, Uganda.
E. A. Lansbury, I. F. M., F.R.E.S., 50A Alston Road, Barnet, Herts.
E. Laptain, Miss J. M., B.SC., The Nature Conservancy, Room 9, Dept. of Botany, The University, Nottingham.
E. Laurie, M. V., M.A., O.B.E., Forest Research Station, Alice Holt, Farnham, Surrey.
E. Lavender, J. H., B.SC., A.R.C.S., Heather Lodge, Burley Road, Brausgore, Christchurch, Hants.
E. Lawrie, J. J., B.SC., 19 Fullerton Drive, Troon, Ayrshire, Scotland.
A. Leatherdale, D., F.R.E.S., Eastfield Lodge, Whitchurch, nr. Pangbourne, Berks.
E. A. LeCren, E. D., The Ferry House, Far Sawrey, Ambleside, Westmorland (*Hon. Sec.*).
A. Le Gay, Brereton, B.SC., University of New England, Armidale, N.S.W., Australia.
A. Lemare, D. W., B.A., Fisheries Dept., Singapore, Malaya.
E. A. Leston, D., F.Z.S., F.R.E.S., 44 Abbey Road, London, N.W.8.
E. A. Lewis, C. B., Institute of Jamaica, East Street, Kingston, Jamaica, B.W.I.
A. Lewis, D. J., M.A., SC.D., Pilgrim's Hall, Brentwood, Essex.
E. Lewis, Miss E. A., M.SC., PH.D.(WALES), Dept. of Education, University College, Swansea, Glamorgan.
E. A. Lewis, J. R., B.SC., Dept. of Zoology, University of Leeds, Leeds, Yorks.
E. A. Lewis, J., 'Spedan', Leckford Abbas, Stockbridge, Hants.
E. Leyton, Dr L., Imperial Forestry Institute, South Parks Road, Oxford.
E. Libbey, R. P., B.SC., 'Laurel Villa', 143 Gaywood Road, King's Lynn, Norfolk.
E. Lind, Miss E. M., B.SC., PH.D., Makerere College, P.O. Box 262, Kampala, Uganda, E. Africa.
A. Linn, I. J., B.SC., Dept. of Zoology, University College, Exeter.
E. A. Lloyd, L. C., Shackerley, Wenlock Road, Shrewsbury, Shrops.
E. A. Lloyd, M. B., B.A., Hull Zoological Laboratory, University of Chicago, Chicago 15, Illinois, U.S.A.
E. A. London Natural History Society, c/o C.P. Castell, Geological Dept., British Museum (Natural History), Cromwell Road, London, S.W.7.
E. Löve, Prof. Askell, Institut Botanique de l'Université de Montreal, 4101 est, rue Sherbrooke, Montreal 36, Canada.
E. Loveless, A. R., PH.D., Dept. of Botany, University College of the W. Indies, Mona, St. Andrew, Jamaica, B.W.I.
E. A. Lovett, M., B.SC., F.R.I.C., F.INST.S.P., Yorkshire Ouse River Board, 21 Park Square South, Leeds, 1.
E. Lovis, J. D., B.SC., 20 Holly Lane West, Banstead, Surrey.
E. Lüdi, Dr W., Gartenstrasse 12, Zollikon, Zürich, Switzerland.

A. LUMSDEN, W. H. R., B.SC., M.B., Virus Research Institute, P.O. Box No. 49, Entebbe, Uganda, E. Africa.
E. LUND, J. W. G., M.SC., PH.D., Freshwater Biological Assoc., The Ferry House, Far Sawrey, Ambleside, Westmorland.
A. MACAN, T. T., 'Stevney', Outgate, Ambleside, Westmorland.
E. MACDONALD, R., B.SC., Benmore House, Dunoon, Argyllshire, Scotland.
E. A. MACFADYEN, A., Dept. of Zoology, University College of Swansea, Singleton Park, Swansea, Glam.
E. MACKAY, J. Ross, 'Ashbrook', 27 Glen-Urquhart Road, Inverness.
E. MACKECHNIE, R., B.SC., 9 Skirving Street, Glasgow, S.1, Scotland.
A. MACKENZIE, J. M. D., F.Z.S., Greyfriars, Greyfriars Garden, St. Andrews, Scotland.
A. MACLAGAN, D. S., D.SC., PH.D., F.R.E.S., West of Scotland Agricultural College, 6 Blythswood Square, Glasgow, C.2.
E. MACLEAY, K. N. G., B.SC., Gordon Memorial College, Khartoum, Anglo-Egyptian Sudan.
E. MACLEOD, Dr Anna M., Heriot-Watt College, Edinburgh, 1.
A. MACLEOD, J., D.SC., Ministry of Agriculture and Fisheries, Field Research Laboratory, Blackford, Carlisle, Cumberland.
A. MACLULICH, D. A., PH.D., 342 Marshall Court, Ottawa, Ontario, Canada.
E. A. MACNAE, W., B.SC., Dept. of Zoology, Rhodes University, Grahamstown, S. Africa.
E. A. MCCONNELL, Mrs R. H., c/o Geological Survey, Lobatsi, Bechuanaland, S. Africa.
A. MCHARDY, J. W., B.SC., Dept. of Agriculture and Forest Zoology, 10 George Square, Edinburgh, 8, Scotland.
E. MCLUCKIE, J., D.SC., Dept. of Botany, The University, Sydney, N.S.W., Australia.
E. MCQUEEN, D. R., M.SC.(N.Z.), c/o Imperial Forestry Inst., South Parks Road, Oxford.
E. A. MCVEAN, D. N., B.SC., B.SC.(AGRIC.), N.D.A., Nature Conservancy, 12 Hope Terrace, Edinburgh, 9.
E. MADGWICK, H. A. I., B.SC., The Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.
A. MADSEN, H., M.SC., Jagtraådets Vildtbiologiske Undersøgelser, Universitetsparken 3, København, Denmark.
E. MAJOR, J., Botany Dept., University of California, Davis, California, U.S.A.
E. MANGHAM, Prof. S., M.A., University College, Southampton.
A. MANN, K. H., B.SC., Dept. of Zoology, The University, Reading, Berks.
A. MANSUETI, R. J., B.S., M.S., SC.D.CAND., Chesapeake Biol. Lab., Maryland Dept. of Research and Education, Solomons, Maryland, U.S.A.
A. MARPLES, Prof. B. J., The Museum, Dunedin, New Zealand.
E. MARSDEN-JONES, E. M., Close Cottage, Littleton Panell, nr. Devizes, Wilts.
E. MARTIN, A. R. H., B.A., 6 Amberley Gardens, Bush Hill Park, Enfield, Middlesex.
E. MASON, E. W., 'Inglenook', 63 King's Road, Richmond, Surrey.
A. MASON, J., B.SC., PH.D., Scottish Home Department, Wood Street, Torry, Aberdeen.
A. MATHESON, C., M.A., B.SC., Dept. of Zoology, National Museum of Wales, Cardiff.
E. MATTHEWS, Prof. J. R., M.A., Dept. of Botany, The University, Old Aberdeen, Scotland.
E. A. MAYOR, Harry, A.C.A., 33 Cleveland Road, Lytham St. Annes, Lancs.
A. MAYR, E., Prof. (Alexander Agassiz Professor of Zoology), Museum Comp. Zool., Cambridge 38, Mass., U.S.A.
E. MEIKLE, R. D., B.A., LL.B., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
A. MELLANBY, Dr K., C.B.E., SC.D., Rothamsted Experimental Station, Harpenden, Herts.
E. A. MELVILLE, R., PH.D., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
E. MERTON, L. F. H., B.A., BM/XKEG, London, W.C.1.
E. MESSERI, Prof. Albina, Via Bolognese 43, Firenze, Italy.
E. METCALF, Dr G., M.A., Botany Dept., King's College, Strand, London, W.C.2.

E. A. Meyerriecks, A. J., Biological Laboratory, Harvard University, Cambridge 38, Mass., U.S.A.
E. A. Michelmore, A. P. G., B.A., Saffron Close, Chudleigh, S. Devon.
A. Middleton, A. D., I.C.I. Game Services, Burgate Manor, Fordingbridge, Hants.
E. A. Middleton, Dr A. R., Biological Labs., University of Louisville, Louisville, Kentucky, U.S.A.
E. A. Midgley, T. W. (since resigned).
E. Migahid, A. M., Botany Dept., Faculty of Science, Fouad I University, Abbassieh, Cairo, Egypt.
A. Miller, R. S., B.A., Harvard University, Biological Labs., 16 Divinity Avenue, Cambridge 38, Mass., U.S.A.
A. Milne, Dr A., M.A., Dept. of Agriculture, King's College, Newcastle-upon-Tyne.
A. Milne, S., B.SC., Dept. of Zoology, The West of Scotland Agricultural College, Blythswood Square, Glasgow, C.2.
E. A. Milne-Redhead, E. W. B. H., M.A., The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey.
E. Mirams, R. V., M.SC., 3 Ingram Road, Rumvera, Auckland, S.E. 3, New Zealand.
E. Misra, Prof. Dr R., PH.D., Dept. of Botany, Banaras Hindu University, Banaras 5, India.
E. Mitchell, B. A., B.SC., c o Forest Research Dept., Klepong, Selangor, Fed. Malay States.
E. Mitchell, G. F., M.A., Dept. of Irish Archaeology, Trinity College, Dublin, Eire.
E. Mobbs, Prof. E. C., O.B.E., M.A., B.SC., Dept. of Forestry, University College of North Wales, Bangor, Caerns., N. Wales.
E. Mohan, N. P., M.A., B.SC., Chief Cons. Officer, Punjab, c/o Imperial Bank of India, Simla, India.
E. Montasir, Prof. Abd El-Halim, PH.D., M.S., Faculty of Science, Ibrahim University, Orman, Giza, Egypt.
A. Montford, H. M., B.SC., 23 Mount Side, Guildford, Surrey.
A. Moon, Prof. H. P., M.A., Dept. of Zoology, University College, Leicester.
E. Mooney, H. F., C.I.E., O.B.E., SC.D., F.L.S., British Middle East Office, British Legation, Beirut, Lebanon.
E. A. Moore, Barrington, 'Stone Acre', Corfe, Taunton, Somerset.
E. Moore, D. M., Botany Dept., Science Laboratories, South Road, Durham City.
E. Moore, Mrs M., B.SC., 17 Staplehurst Road, Hall Green, Birmingham, 28.
A. Moore, N. W., B.A., PH.D., The Nature Conservancy, Furzebrook Research Station, Wareham, Dorset.
E. Moore, R. M., M.SC., 94 Arthur Circle, Forrest, Canberra, A.C.T., Australia.
A. Morley, B. D. W., B.A., F.L.S., 47 Downshire Hill, Hampstead, N.W.3.
E. Morris, Miss F. M., B.SC., 7 Ravenstone Drive, Sale, Cheshire.
A. Morris, K. R. S., PH.D., The Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancs.
E. A. Moynahan, E. J., M.R.C.S., Wayside, Jordans, Beaconsfield, Bucks.
A. Muir, R. C., 138 Upper Fant Road, Maidstone, Kent.
A. Mundie, J. H., B.SC., The Ferry House, Far Sawrey, Ambleside, Westmorland.
A. Murphy, D. H., Zoology Dept., Science Labs., South Road, Durham.
E. A. Murphy, P. W., B.AGR.SC., D.PHIL., Rothamsted Experimental Station, Harpenden, Herts.
A. Neal, E. G., B.SC., 'Foxcombe', Greenway Road, Taunton, Somerset.
A. Nelmes, E. M., B.A., 27 Westbourne Avenue, Acton, London, W.3.
E. Newbould, P. J., Botany Dept., University College, Gower Street, London, W.C.1.
E. A. Newton, Prof. Lily, M.SC., PH.D., Dept. of Botany, University College of Wales, Aberystwyth, Wales.
A. Nichols, Prof. J. E., PH.D., Institute of Rural Science, Penglais, Aberystwyth.
A. Nicholson, E. M., 13 Upper Cheyne Row, London, S.W.3.
E. Nicholson, I. A., M.SC., B.SC. (AGR.), Hill Farming Research Organization, 48 Palmerston Place, Edinburgh 12.
E. A. Nielsen, C. O., D.PHIL., Molslaboratoriet, Femmöller, Denmark.

E. Norman, M. J. T., B.Sc., Land Research and Regional Survey Section, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T., Australia.
A. Norris, C. A., Clent House, Clent, Worcestershire.
A. Norris, K. R., M.Sc., c/o C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T., Australia.
E. Northumberland, Durham and Newcastle-upon-tyne Nat. Hist. Soc., Hancock Museum, Barras Bridge, Newcastle-upon-Tyne, 2.
E. O'Connor, Miss W. M. T., B.Sc., Hartley Botanical Laboratories, The University, Liverpool, 3.
E. A. Odhiambo, T. R., Kawanda Research Sta., P.O. Box 265, Kampala, Uganda.
E. Oliver, W. R. B., D.Sc., 26 Ventnor Street, Seatown, Wellington, E.5, New Zealand.
A. Omer-Cooper, Prof. J., M.A., M.Sc., Rhodes University College, Grahamstown, S. Africa.
E. A. Orr, H. R., Technical College, Longport Street, Canterbury, Kent.
E. Orshan, G., Dept. of Botany, The Hebrew University, Jerusalem, Israel.
E. Osborn, Prof. T. G. B., 22 Hardwicke Street, Balwyn, Melbourne, Victoria, Australia.
E. Osmaston, H., M.A., Forest Office, Fort Portal, Uganda, E. Africa.
E. Osvald, Prof. K. Hugo, Royal Agricultural College, Uppsala 7, Sweden.
E. Ovington, J. D., Ph.D., Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancashire.
E. Padgham, Mrs J., B.Sc., 87 Halesworth Road, Lewisham, London, S.E.13.
E. A. Pallant, D., B.Sc., 8 Andover Road, Southsea, Hants.
E. Park, K. J. F., The Nature Conservancy, Moor House, Garrigill, Alston, Cum.
E. A. Park, Dr O., Zoological Dept., Northwestern University College of Liberal Arts, Evanston, Ill., U.S.A.
E. Parke, Dr Mary, The Laboratory, Citadel Hill, Plymouth.
E. Parker, R. E., B.Sc., Dept. of Botany, The Queen's University, Belfast.
E. Parkinson, Mrs M., M.A., 13 Southernhay West, Exeter.
A. Parry, D. A., Ph.D., King's College, Cambridge.
Paterson, Mrs H. M., 61 Smarts Road, Gravesend, Kent (*Associate Member*).
E. A. Patten, B. C., Jr., 7710 Second Street, Dexter, Mich., U.S.A.
A. Paviour-Smith, Miss K., M.Sc., Bureau of Animal Population, The Botanic Garden, High Street, Oxford.
A. Peacock, Prof. A. D., D.Sc., F.R.S.E., University College, Dundee, Scotland.
E. A. Peake, J. F., 17 Tillet Road, Norwich, Norfolk.
E. Pearsall, Prof. W. H., F.R.S., Botany Dept., University College, Gower Street, London, W.C.1.
E. Pearson, M. C., B.Sc., Dept. of Botany, The University, Nottingham.
E. Pelton, J. F., Ph.D., Botany Dept., Butler University, Indianapolis, Indiana, U.S.A.
E. Penston, Dr Norah L., F.L.S., Bedford College, Regent's Park, London, N.W.1.
A. Pentelow, F. T. K., Old Slade Lane, Iver, Bucks.
A. Percival, Prof. E., Canterbury University College, P.O. Box 1471, Christchurch, New Zealand.
E. A. Perkins, E. J., Post Office, Cross Keys, Hereford.
E. Perraton, C. J., B.A., M.A., M.I. Biol., 60 East Street, Havant, Hants.
E. Perrin, R. M., B.A., School of Agriculture, Downing Street, Cambridge.
E. Perring, F. H., B.A., 180 Cherry Hinton Road, Cambridge.
E. Perry, R. A., B.Sc., 7 Quick Street, Ainslie, Canberra City, A.C.T., Australia.
E. Petch, C. P., M.A., M.B., 10 Abinger Avenue, Cheam, Surrey.
E. Peterken, J. H. G., F.L.S., 73 Forest Drive East, Leytonstone, London, E.11.
E. A. Phillips, Prof. J. F. V., University College of the Gold Coast, Achimota, P.O., Accra, B.W. Africa.
E. Phillips, Miss M. E., M.Sc., 4 Morella Road, Clifton Gardens, Sydney, N.S.W., Australia.
E. Pichi-Sermolli, Prof. R., Istituto Botanica dell' Universita, Via Lamarmora 4, Firenze, Italy.

E. Pielou, Mrs E. C., B.SC., c/o Dominion Entomological Laboratory, Summerland, British Columbia.
A. Pielou, Dr D. P., c/o Dominion Entomological Laboratory, Summerland, British Columbia.
E. Pigott, C. D., M.A., PH.D., Dept. of Botany, The University, Sheffield, 10.
E. A. Pitelka, F. A., PH.D., Museum of Vertebrate Zoology, University of California, Berkeley 4, California, U.S.A.
E. Pitman, P. B., B.SC., 3 Beverley Gardens, Ensbury Park, Bournemouth, Hants.
E. Poel, Dr L. W., Dept. of Botany, The University, St. Andrews, Scotland.
E. Polunin, Prof. N., D.PHIL., D.SC., Dept. of Botany, College of Arts and Sciences, Bagdad, Iraq.
A. Pontin, A. J., B.A., 15 Southdale Road, Oxford.
E. A. Poore, M. E. D., PH.D., Hunting Aero Surveys Ltd., c/o Dept. of Agriculture, Nicosia, Cyprus.
E. Pope, Miss E. C., M.SC., The Australian Museum, College Street, Sydney, Australia.
E. A. Potts, W. H., M.A., 45 Green Moor Links, Winchmore Hill, London, N.21.
E. A. Pough, R. H., American Museum of Natural History, Central Park West at 79th Street, New York 24, N.Y., U.S.A.
E. Powell, Miss Doris, M.SC., Aldersyde, Reigate, Surrey.
E. A. Powell, H. T., B.SC., Marine Station, Millport, Isle of Cumbrae, Scotland.
A. Pradhan, Dr S., Entomology Division, Indian Agricultural Research Institute, New Delhi, India.
E. Pratt, Dr C. A., Botany Dept., Imperial College of Science and Technology, London, S.W.7.
A. Preston, F. W., Preston Laboratories, Box 847, Butler, Pennsylvania, U.S.A.
A. Price, Miss K. L. H., Hillside, Headington Hill, Oxford.
A. Price Jones, Dr D., Fernhurst, nr. Haslemere, Surrey.
A. Prideaux, R. C., Claigan, Dunvegan, Isle of Skye, Scotland.
E. Prime, C. T., M.A., PH.D., F.L.S., 147 Upper Selsdon Road, Sanderstead, S. Croydon, Surrey.
E. Pritchard, N. M., 1 Lankers Drive, Harrow, Middlesex.
E. Pritchard, T. O., Dept. of Botany, The University, Leeds 2.
E. Proctor, M. C. F., M.A., The Nature Conservancy, School of Agriculture, University College of North Wales, Bangor, Caerns.
E. A. Prychodko, W., c/o Detroit Inst. of Cancer Research, 4811 John R. Street, Detroit 1, Michigan, U.S.A.
A. Pyefinch, K. A., Brown Trout Research Laboratory, Faskally House, Pitlochry, Perthshire.
A. Putnam, C. D., B.A., F.R.E.S., 'Davenants', Sible Hedingham, Halstead, Essex.
A. Radway Allen, K., Fisheries Laboratory, 27 Wingfield Street, Wellington, New Zealand.
E. Raggio, M., 25 de Mayo 316, Esc. 2, Piso 1, Buenos Aires, Argentina.
E. Rains, A. B., B.SC., 28 Vicarage Lane, Humberstone, Leicester.
E. Ramsbottom, J., M.A., O.B.E., British Museum (Natural History), Cromwell Road, London, S.W.7.
A. Rand, R. W., B.SC., Office of the Superintendent of the Government, Guano Islands, P.O. Box 251, Cape Town, S. Africa.
E. Ranwell, D. S., PH.D., B.SC., Furzebrook Research Station, nr. Wareham, Dorset.
E. Ratcliffe, D., B.SC., Dept. of Botany, The University, Sheffield, 10.
E. Ratcliffe, D. A., PH.D., B.SC., 72 Newton Road, Carlisle.
A. Ratcliffe, F. N., B.A., C.S.I.R.O., Wildlife Survey Section, P.O. Box 109, City, Canberra A.C.T., Australia.
A. Raw, Frank, B.SC., Rothamsted Experimental Station, Harpenden, Herts.
A. Raymont, Prof. J. E. G., B.SC., A.M., Dept. of Zoology, University College, Southampton.
E. Reed, Prof. J. F., PH.D., The University of New Hampshire, Dept. of Botany, Durham, New Hampshire, U.S.A.

E. Rees, T. Kenneth, D.I.R. Division, Board of Trade, Horseguards' Avenue Whitehall, S.W.1.
E. Rees, W. J., PH.D., Botany Dept., The University, Edgbaston, Birmingham, 15.
E. Regel, Dr C., Stiftingtalstrasse 69, Graz, Austria.
E. A. Reid, D. A., B.SC., 19 High Street, Leighton Buzzard, Beds.
A. Reid, R. E. H., B.SC., Dept. of Geology, Queen's University, Belfast.
E. A. Renouf, Prof. L. P. W., University College, Cork, Eire.
E. Reynolds, E. R. C., B.SC., A.R.C.S., 25A Egmont Road, Sutton, Surrey.
A. Reynoldson, T. B., SC.D., PH.D., Dept. of Zoology, University College of North Wales, Bangor, N. Wales.
E. Rhodes, Prof. A. D., Forestry Dept., Massachussetts State College, Amherst, Mass., U.S.A.
A. Ribbands, C. R., M.A., Rothamsted Experimental Station, Harpenden, Herts.
E. Ribbons, B. W., Dept. of Botany, The University, Glasgow, W.2, Scotland.
E. A. Richards, Prof. O. W., M.A., D.SC., Zoology Dept., Imperial College of Science, S. Kensington, London, S.W.7.
E. Richards, P. T., The Imperial College of Tropical Agriculture, Trinidad, British West Indies.
E. Richards, Prof. P. W., M.A., SC.D., Dept. of Botany, University College, Bangor.
E. Richards, Mrs S. A., M.A., Coed Menai, Upper Bangor, Caern.
A. Richards, Dr W. S., c/o M.C.P.S., Wad El Hur, Anglo-Egyptian Sudan.
E. Richardson, J. A., M.SC., Dept. of Botany, King's College, Newcastle-upon-Tyne.
E. Richardson, W. D., B.SC., c/o The Imperial College of Tropical Agriculture, St. Augustine, Trinidad, B.W. Indies.
E. Ritchie, J. C., Dept. of Botany, University of Manitoba, Winnipeg, Canada.
A. Roberts, B. B., Scott Polar Research Institute, Lensfield Road, Cambridge.
E. Roberts, Miss E., 6 Kingsbury Street, Marlborough, Wilts.
A. Roberts, H., B.SC., c/o 'Greystones', Woodfield, Dursley, Glos.
E. Roberts, H. A., B.SC., 39 Newbold Road, Wellesbourne, Warwick.
E. Roberts, Prof. R. Alun, Agricultural Dept., University College, Bangor, N. Wales.
E. Robertson, A. G., B.SC., 2 Westfield Park, Bristol, 6.
E. Robertson, D. A., B.SC., Broomhaugh Cottage, Riding Mill, Northumberland.
E. Robertson, Mrs E. T., B.SC., F.G.S., Dept. of Botany, University College of the West Indies, Mona, St. Andrew, Jamaica, B.W.I.
A. Robertson, I. A. D., B.SC., P.O. Box 37, Abercorn, N. Rhodesia.
E. Robertson, R. A., B.SC., Macaulay Institute for Soil Research, Aberdeen, Scotland.
E. Robertson, R. N., The Botany Dept., The University, Sydney, N.S.W., Australia.
E. A. Robertson, V. C., M.A., B.SC., Tanglin, Second Avenue, Frinton-on-Sea, Essex.
E. Robson, N. K. B., B.SC., Dept. of Botany, Royal Botanic Gardens, Edinburgh, 4, Scotland.
E. A. Roffey, J., B.SC., A.R.C.S., Desert Locust Survey, P.O. Box 231, Asmara, Eritrea.
E. Rorison, I. H., University of Nottingham, School of Agriculture, Sutton Bonington, Loughborough.
E. Rosayro, R. A. de, B.A., B.SC., Forest Dept., P.O. Box 500, Colombo, Ceylon.
E. Rose, F., The Forge House, East Malling, Maidstone, Kent.
Rosenberg, Dr Marie (Mrs Burton), *see under* Dr M. B. Burton.
E. Ross, R., B.A., British Museum (Natural History), Cromwell Road, London, S.W.7.
A. Rothschild, The Hon. Miriam, Ashton Wold, Peterborough.
A. Rothwell, Mrs D. R., PH.D., Pin Mill, Brow House, Howey Lane, Frodsham, nr. Warrington, Lancs.
E. Round, F. E., B.SC., Botany Dept., The University, Edgbaston, Birmingham, 15.
E. Rowntree, J. R. B., M.A., Hilla Green Farm, Hackness, Scarborough, Yorks.
E. Rübel, Dr E., Zürichbergstrasse 38, Zürich 44, Switzerland.
E. Russell, Dr E. W., Dept. of Agriculture, Parks Road, Oxford.
E. Russell, Dr R. S., Dept. of Agriculture, Parks Road, Oxford.
E. Russell-Wells, Miss B., PH.D., Biology Dept., Lancing College, Shoreham, Sussex.

E. Rutter, Dr A. J., Botany Dept., Imperial College of Science, S. Kensington, London, S.W.7.
A. Ryland, J. S., Marine Biology Station, Menai Bridge, Anglesey.
A. Rzóska, Julian R. D., Gordon Memorial College, Khartoum, A.-E. Sudan.
E. Sagar, G. R., Dept. of Agriculture, Parks Road, Oxford.
E. Saksena, M. R., ph.d., m.sc., Botany Dept., Osmania University, Hyderabad, Deccan, India.
E. A. Sale, G. N., b.sc., The Nature Conservancy, 19 Belgrave Square, London, S.W.1.
E. Salisbury, Sir Edward J., c.b.e., d.sc., f.r.s., Royal Botanic Gardens, Kew, Surrey.
E. A. Salt, G., d.sc., sc.d., King's College, Cambridge.
A. Salt, Dr G. W., Dept. of Zoology, University of California, Davis, Calif., U.S.A.
A. Sandison, Miss E. D., b.sc., Dept. of Zoology, University College, Ibadan, Nigeria, B. W. Africa.
E. Sands, Mrs K., ph.d., Botany Dept., Imperial College of Science and Technology, Dept. of Botany, Prince Consort Road, London, S.W.7.
E. Sangster, R. G., Assistant Conservator of Forests, P.O. Box 31, Entebbe, Uganda, E. Africa.
A. Sankey, J. H. P., b.sc., Juniper Hall Field Centre, Dorking, Surrey.
E. Sankey, Mrs V. O., ph.d., 3 Glenrose, Mickleham, Dorking, Surrey.
E. Sansom, Miss J. M., b.sc., 149 Sandbanks Road, Parkstone, Dorset.
E. Santapau, Rev. H., ph.d., Biology Dept., St. Xavier's College, Cruikshank Road, Bombay 1, India.
E. Sappa, Dr Francesco, Istituto Botanica, Viale Mattioli 31, Turin, Italy.
A. Satchell, J. E., b.sc., Merlewood Research Station, Grange-over-Sands, N. Lancs.
E. A. Saunders, J. T., m.a., University College, Ibadan, Nigeria, W. Africa.
A. Savage, R. M., Rosendaui, Parkgate Crescent, Hadley Wood, Barnet, Herts.
E. Savidge, J. P., 'Millwood', Spital, Wirral, Cheshire.
E. Schelpe, E. A. C. L. E., d.phil., m.sc., Dept. of Botany, University of Cape Town Rondesbosch, S. Africa.
E. A. Schjøtz-Christansen, K. B., Naturhistorisk Museum, Aarhus, Denmark.
E. Scott, G. A. M., 'Snob Cottage', Rickarton, Kincardineshire.
E. Scurfield, G., ph.d., Botany Dept., The University of Manchester, Manchester.
E. A. Segadas-Vianna, F., b.sc., Rua Rainha Guilhermina, 83 Leblon, Rio de Janeiro, Brazil.
E. Shanks, Royal E., Botany Dept., University of Tennessee, Knoxville, Tennessee, U.S.A.
E. Shaw, Miss M. S., b.sc., Woodlea, Honley, nr. Huddersfield.
E. A. Sheals, J. G., b.sc., Entomology Dept., Ministry of Agriculture and Fisheries and Food, 'Woodthorne', Wolverhampton, Staffs.
E. Sheldon, J., b.sc., 'Greystones', Bately Avenue, Gorleston-on-Sea, Norfolk.
A. Serck-Hanssen, T., Paradis, Bergen, Norway.
E. Sherwood, E. G. P., m.a., P.O. Box 4930, N'g Ong, Kenya Colony.
E. Side, Mrs A. G., 107 London Road, Stone, Dartford, Kent.
A. Side, K. C., f.r.e.s., 107 London Road, Stone, Dartford, Kent.
E. A. Simpson, C., 44 Tinshill Road, Cookridge, Leeds, 16.
E. Simpson, N. Douglas, m.a., f.l.s., 3 Cavendish Road, Bournemouth, Hants.
E. Singh, B. N., d.sc., Institute of Crop Physiology, 1A Sultanpur Road, Lucknow, India.
A. Singh, C. P., b.sc., m.sc., f.l.s., Zoology Dept., Agra College, Agra, India.
E. Sinker, C. A., b.a., Malham Tarn Field Centre, Settle, Yorks.
E. A. Skellam, J. G., m.a., 30 The Little Boltons, S. Kensington, London, S.W.10.
A. Sladen, Mrs W., b.sc., c/o The Rockefeller Foundation, 49 West 49th Street, New York 20, U.S.A.
E. Slater, W. G., University Dept. of Botany, Oxford.
E. Smith, A. H. V., b.sc., 96 Berkshire Gardens, Palmer's Green, London, N.13.
E. Smith, Miss P. M., b.sc., Osmotherley, Bromsgrove, Worcs.

A. SMITH, Dr R. F., M.S., PH.D., 112 Agriculture Hall, University of California, Berkeley 4, California, U.S.A.
A. SMYLY, W. J. P., B.SC., The Ferry House, Far Sawrey, Ambleside, Westmorland.
E. A. SMYTH, J. C., PH.D., 24 Pentland Terrace, Edinburgh, 10.
E. A. SOLOMON, M. E., M.SC., D.S.I.R., Pest Infestation Laboratory, London Road, Slough, Bucks.
A. SOUTHERN, H. N., B.A., Bureau of Animal Population, Botanic Garden, High Street, Oxford.
A. SOUTHWOOD, T. R. E., B.SC., PH.D., A.R.C.S., Imperial College of Science and Technology, Field Station, Silwood Park, Sunninghill, Berks.
E. SOWERBY, W. B. H., B.SC., 24 Windsor Grove, Morecambe, Lancs.
E. SPEDDING, Mrs B. N., M.A., B.SC., Holm Peigh, Cookham Rise, Berkshire.
E. A. SPENCE, A. C., M.R.C.S., L.R.C.P., 24 Wellington Road, London, N.W.8.
E. SPENCE, D. H. N., B.SC., Botany Dept., The University, Glasgow, W.2.
E. SPOONER, G. M., M.A., M.B.E., Marine Biological Laboratory, Citadel Hill, Plymouth.
A. SPOONER, Mrs G. M., Fiveoaks, Crapstone, Yelverton, Devon.
E. SPORNE, K. R., M.A., PH.D., The Botany School, Downing Street, Cambridge.
E. A. STAMP, Prof. L. Dudley, C.B.E., Ebbingford Manor, Bude Haven, Cornwall.
E. STANBURY, Miss F. A., Plymouth and Davenport Technical College, Tavistock Road, Plymouth.
A. STEPHEN, Dr A. C., Royal Scottish Museum, Edinburgh.
E. STEPHENSON, Prof. T. A., F.R.S., D.SC., Dept. of Zoology, University College of Wales, Aberystwyth.
A. STEPHENSON, Prof. W., Dept. of Zoology, University of Queensland, Brisbane, Australia.
E. STEVENS, A. J., B.A., 25 Wings Road, Upper Hale, Farnham, Surrey.
A. STEVENS, D. M., Dept. of Zoology, West Mains Road, Edinburgh, 9.
E. STEVENSON, Miss E. H., 28 Foxcombe Road, Weston, Bath, Somerset.
E. STEWARD, V. I., 5 Seafield Avenue, Aberdeen, Scotland.
E. STEWART, Dr R. R., M.A., Gordon College, Rawalpindi, Pakistan.
E. STILES, Prof. W., M.A., SC.D., F.R.S., 'Elsley Lodge', Tilehurst-on-Thames, Reading, Berks.
E. STONE, P. L., Southmead Cottage, Burley Lodge, Burley, Nr. Ringwood, Hampshire.
A. STOWER, W. J., B.SC., Desert Locust Control, P.O. Box 231, Asmara, Eritrea.
A. STRICKLAND, A. H., M.A., Plant Path. Lab., Ministry of Agriculture, Milton Road, Harpenden, Herts.
E. A. SUMMERHAYES, V. S., B.SC., Royal Botanic Gardens, Kew, Richmond, Surrey (*Hon. Treasurer*).
E. SUVATABANDHU, Kasin, B.SC., Botanical Section, Dept. of Agriculture, Bangkok, Thailand (Siam).
A. SVENDSEN, J. A., B.SC., 57 University Road, Belfast.
E. SWANN, E. L., 282 Wootton Road, King's Lynn, Norfolk.
A. SWYNNERTON, G. H., Game Preservation Dept., Nyamungu, Moshi, Tanganyika Territory.
E. TALLIS, J. H., 34 Athenaeum Road, Whetstone, London, N.20.
TALLANTIRE, Miss A. C., B.SC., P.O. Box 262, Kampala, Uganda, E. Africa (*Associate Member*).
E. A. TASMANIAN BIOLOGICAL SURVEY, Tasmanian Museum and Art Gallery, Hobart, Tasmania.
A. TAYLOR, D. J., B.SC., West African Cacao Research Institute, Tafo, Gold Coast, W. Africa.
E. TAYLOR, F. J., M.SC., Dept. of Botany, Queen Mary College, Mile End Road, London E.1.
E. TAYLOR, G., D.SC., British Museum (Natural History), Cromwell Road, London, S.W.7.
E. TAYLOR, Miss M. H., B.SC., Belmont Farm, Clarendon, nr. Salisbury, Wilts.
E. TEDD, H. Griffith, Bottor Cottage, Hennock, Bovey Tracy, Devon.

A. Tener, J. S., M.A., Canadian Wildlife Service, Dept. of Northern Affairs and Natural Resources, Ottawa, Ontario, Canada.
A. Tevis, Lloyd P., Dept. of Zoology, University of California, Davis, California, U.S.A.
E. Thoday, Prof. D., M.A., SC.D., F.R.S., 'Haulfre', Park Crescent, Llanfairfechan, N. Wales.
E. A. Thomas, A. K., B.SC., Bishop Vesey's Grammar School, Sutton Coldfield, Warwickshire.
E. Thomas, A. S., D.SC., Goodings Cottage, Woodland St. Mary, Newbury, Berks.
E. Thomas, H. Hamshaw, M.B.E., SC.D., F.R.S., Botany School, Cambridge.
A. Thomas, I. F., B.A., The School, Oundle, Peterborough.
A. Thomas, M. Pugh, B.SC., 35 Meols Drive, Hoylake, Cheshire.
A. Thompson, H. V., B.SC., Ministry of Agriculture and Fisheries, Hook Rise, Tolworth, Surbiton, Surrey.
A. Thomsen, H. P., PH.D., M.S., R.H. 3, Box 406, Beloit, Wisconsin, U.S.A.
Thornton, I. W. B., B.SC., University College of Khartoum, Khartoum, Sudan. (*Associate Member*).
E. Thorp, Mrs D. A., c/o Prof. Thorp, Sydney University, N.S.W., Australia.
Thorpe, W. H., SC.D., Jesus College, Cambridge (*Associate Member*).
E. Thurston, Miss J. M., B.SC., Rothamsted Experimental Station, Harpenden, Herts.
Tidmarsh, C. E. M., PH.D., Grootfontein College of Agriculture (Pasture Research),
E. Middelburg, Cape Province, S. Africa.
Tincker, M. A. H., M.A., D.SC., Hort. Dept., North of Scotland College of Agric.,
E. 41½ Union Street, Aberdeen.
A. Tjønneland, A., c/o E.A.F.R.O., P.O. Box 343, Jinja, Uganda.
E. Todd, Miss M. A., M.SC., c/o Agent General for Victoria, Victoria House, Strand, London, W.C.2.
E. A. Todorovic, Maksim, DIP. BIOL.(BELGRADE), Institut za Ekologiju, 29 Novembra, 100, Belgrad, Yugoslavia.
E. A. Tonolli, Dr. V., Istituto Italiano di Idrobiologia, Pallanza (Novara), Italy.
A. Toschi, Prof. A., Laboratorio di Zoologia, Via S. Giacomo 9, Bologna, Italy.
E. A. Trapnell, C. G., B.A., E. African Agric. and Forestry Res. Organ., P.O. Box 21, Kikuyu, Kenya.
E. Troll, Prof. C., Geographical Dept., University of Bonn, Bonn, Germany.
E. Trump, E. C., B.SC., Tsetse Survey and Control, Veterinary Dept., P.O. Kabete, Kenya.
A. Turnbull, A. L., B.SC.F., M.F., 414 Banbury Road, Oxford.
E. Turner, Prof. J. S., PH.D., Botany Dept., The University, Melbourne, Victoria, Australia.
E. A. Turner, Miss M. A., Belford House, Kennford, nr. Exeter.
E. A. Turrill, W. B., D.SC., Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey (*Vice-President*).
E. Tutin, Prof. T. G., M.A., Dept. of Botany, University College, Leicester.
A. Tutin, Mrs T. G., PH.D., Dept. of Botany, University College, Leicester.
E. Tüxen, Prof. Reinhold, Schinnaerlandsstr. 6, Stolzenau/Weser, Germany.
E. Tyler-Smith, M. A., 'Strathallan', Broadway, Southbourne, Bournemouth.
E. Uren, Miss E. M., B.SC., The University, Southampton.
A. Uvarov, B. P., C.M.G., D.SC., British Museum (Natural History), Cromwell Road, London, S.W.7.
E. Valentine, Prof. D. H., PH.D., University Dept. of Botany, Science Laboratories South Road, Durham.
A. Varley, Prof. G. C., Hope Dept., University Museum, Parks Road, Oxford (*President*).
E. Vaughan, R. E., B.SC., PH.D., A.R.C.S., The Terraces, Phoenix, Mauritius.
E. A. Vesey-Fitzgerald, L. D. E. F., M.B.E., B.SC., International Red Locust Control Service, Abercorn, N. Rhodesia.
E. de Vesian, Miss D. E., 3 Lansdown Terrace, Cheltenham.

A. VEVERS, Dr H. G., M.B.E., Zoological Society of London, Regents Park, London, N. W. 1.
A. VICKERS, G. G., M.SC., Zoology Dept., University College, Exeter.
A. VINCENT, Mrs M. H., B.SC., 1 Manor Road, South Hinksey, nr. Oxford.
A. VIZOSO, Mrs M. R., B.A., 11 Churchdale Court, Harvard Road, Chiswick, London, W.4.
A. VOGT, W., 510 Madison Avenue, New York 22, N.Y., U.S.A.
A. VOÛTE, Dr Alexander D., ITBON, Kemperbergerweg 11, Arnhem, Netherlands.
E. VYVYAN, M. C., M.A., Trevedran, Wateringbury, Kent.
E. WADHAM, Prof. S. M., School of Agriculture, Melbourne University, Victoria, Australia.
E. WALKER, D., Clare College, Cambridge.
E. WALKER, F. T., B.SC., Institute of Seaweed Research, Inveresk Gate, Musselburgh, Midlothian.
A. WALKER, Miss Jennifer M., B.SC., Flatford Mill, East Bergholt, nr. Colchester, Essex.
E. A. WALKER, Peter T., B.SC., D.I.C., Colonial Insecticide Research, P.O. Box 204, Arusha, Tanganyika, East Africa.
E. WALLACE, T. J., Goodmans, Furley, Membury, nr. Axminster, Devon.
A. WALOFF, Miss Nadejda, PH.D., Dept. of Zoology, Imperial College of Science, Prince Consort Road, London, S.W.7.
E. WALTERS, S. M., B.A., Botany School, Downing Street, Cambridge.
E. WALTON, Prof. J., D.SC., SC.D., LL.D., Dept. of Botany, The University, Glasgow.
E. WANSTALL, P. J., Dytchleys, Coxtie Green, Brentwood, Essex.
E. WARBURG, E. F., M.A., PH.D., University Dept. of Botany, South Parks Road, Oxford.
E. A. WARD, C. J., B.SC. (S.A.), B.SC. (HONS. NATAL), P.O. Box 25, Mtubatuba, Zululand, South Africa.
E. A. WARD, Ronald A., PH.D., Dept. of Biology, Gonzaga University, Spokane, 2, Washington, U.S.A.
E. WATSON, E. V., B.SC., PH.D., Dept. of Botany, University of Reading, Reading.
A. WATSON, J. S., B.A., D.S.I.R., Animal Ecology Section, Wellington, New Zealand.
E. WATSON, W., D.SC., Cedene, Cheddon Road, Taunton, Somerset.
E. A. WATSON-WALKER, J., B.SC., 12 The Bowley, Diseworth, Derby.
E. A. WATT, A. S., PH.D., The Botany School, Downing Street, Cambridge.
E. A. WATT, Mrs W. Boyd, 'San Simeon', 52 Wimborne Road, Bournemouth.
E. A. WATTERSON, J. G., B.SC., Tsetse Survey and Reclamation Dept., P.O. Box 668, Tanga Province, Tanganyika Territory.
E. WATTS, W. A., B.A., School of Botany, Trinity College, University of Dublin, Dublin, Eire.
E. A. WAUTIER, Prof. J., D.SC., Laboratoire de Zoologie Écologique, Faculté des Sciences, Lyons, France.
E. WEBB, Prof. D. A., PH.D., School of Botany, Trinity College, Dublin, Eire.
E. WEBSTER, J. R., B.SC., A.R.C.S., M.I.BIOL., 15 Lyndhurst Close, Plomer Hill, High Wycombe, Bucks.
WELCH, Mrs B., 203 Lichfield Court, Richmond, Surrey (*Associate Member*).
A. WERTH, Miss I., Dept. of Zoology, The University, Leeds, 2.
E. WEST, Dr Cyril, The Cowl House, Holt Wood, Aylesford, Kent.
E. WEST, R. G., 34 Elwill Way, Beckenham, Kent.
E. A. WEST WALES FIELD SOCIETY, Orielton, Pembroke, Pembs.
A. WESTCOTT, Miss M. V., M.SC., 20 Linden Road, Redland, Bristol, 6.
E. WHITE, Miss A., John Innes Hort. Inst., Bayfordbury, Hertford, Hertfordshire.
E. WHITE, D. S., B.SC., 44 The Park, Kingswood, Bristol.
E. WHITE, F., B.A., Imperial Forestry Institute, South Parks Road, Oxford.
A. WHITE, Miss K. M., B.SC., PH.D., Glastonbury, Boyn Hill Avenue, Maidenhead, Berks.
E. A. WHITE, O. M., 78 Eastdale Road, Nottingham.
A. WHITE, P. H. F., M.A., Science Schools, Harrow School, Harrow, Middlesex.

E. WHITEHEAD, F. H., B.A., D.PHIL., University Dept. of Botany, South Parks Road, Oxford.
E. WHITEHOUSE, H. L. K., M.A., PH.D., Botany School, Downing Street, Cambridge.
E. WHYTE, Dr R. O., c/o Plant Prod. Branch, F.A.O. Viale delle Terme di Caracalla, Rome, Italy.
E. WIEHE, P. O., Sugar Industry Research Institute, Reduit, Mauritius.
E. WILKINS, D. A., B.SC., Scottish Soc. for Research in Plant Breeding, Pentlandfield, Roslin, Midlothian.
E. A. WILLIAMS, C. B., SC.D., Ard Insh, Kincraig, Inverness-shire.
A. WILLIAMS, G., B.SC., Zoology Dept., The University, Reading, Berks.
E. WILLIAMS, O. G., B.SC., Assistant Agricultural and Food Attaché, British Embassy, Washington, U.S.A.
E. A. WILLIAMS, R. B., B.A., M.S., Division of Oceanography, U.S.N. Hydrographic Office, Suitland, Md., U.S.A.
WILLIAMS, R. D., B.SC., PH.D., 92 Loxley Road, Stratford-upon-Avon, Warwicks. (*Associate Member*).
E. WILLIAMS, Mrs S. S., B.SC., Grassland Research Station, Drayton, Stratford-on-Avon, Warwicks.
E. WILLIAMSON, A. C., B.SC., Forest Dept., Belize, Brit. Honduras.
E. A. WILLIAMSON, H. M., Fairfield, Pullen's Lane, Oxford.
E. WILSON, I. E., B.SC., Agricultural Institute, Bambui, Bamenda, British Cameroons, West Africa.
E. WILSON, J. M., M.A., Science Dept., The British Council, 65 Davies Street, London, W.1.
E. WILSON, J. W., M.A., D.PHIL., Dept. of Botany, The University, Reading, Berks.
A. WILSON, Mrs P. M. W., M.A., D.PHIL., 7 Denmark Road, Reading, Berks.
E. WILSON, Miss S., B.SC., Biology Dept., College of Technology and Commerce, The Newarkem, Leicester.
E. WILSON MAYNE, W., B.SC., Scientific Officer, Messrs. Kanan Devans Hills Produce Co. Ltd., Munnar P.O., Travancore, India.
A. WINTERBOTTOM, J. M., PH.D., Box 1616, Cape Town, S. Africa.
E. WOOD, G. H. S., M.A., c/o Imperial Forestry Institute, South Parks Road, Oxford.
E. A. WOODELL, S. R. J., B.SC., 198 Holland Park Avenue, London, W. 11.
E. WOODHEAD, Norman, M.SC., Dept. of Botany, University College, Bangor, N. Wales.
E. A. WORDEN, Prof. A. N., M.A., B.SC., Cromwell House, Huntingdon.
E. WRIGHT, A. C. S., D.S.I.R., Soil Bureau, Aotea Quay, Wellington, New Zealand.
E. WRIGHT, Mrs B. I., B.SC., 'Ecclesfield', 176 Stockbridge Road, Winchester, Hants.
E. WRIGHT, Dr F. R. Elliston, Braunton, N. Devon.
E. WRIGHT, Miss J. K., B.SC., Botany Dept., University College, Gower Street, London, W.C.1.
E. A. YAPP, W. B., M.A., Dept. of Zoology, The University, Edgbaston, Birmingham, 15.
E. ZEHETMAYR, J. W. L., Warriston, Ballplay Road, Moffat, Dumfriesshire.
E. ZEIST, Dr W. van, Inst. for Biological Archaeology, Poststraat 6, Groningen, Holland.
E. ZINDEREN BAKKER, Dr E. M. van, University of the Orange Free State, Bloemfontein, S. Africa.
E. ZOHARY, Dr M., Dept. of Botany, Hebrew University, Jerusalem.

OFFICERS AND COUNCIL OF THE SOCIETY FROM JANUARY 5TH, 1956

President: G. C. VARLEY.

Vice-Presidents: N. A. BURGES, C. DIVER.

Hon. Treasurers: V. S. SUMMERHAYES, C. E. HUBBARD (subscriptions should be paid to C. E. HUBBARD).

Hon. Secretaries: E. D. LECREN, C. H. GIMINGHAM.

Hon. Editor of the Journal of Ecology: H. GODWIN.

Hon. Assistant Editor: D. E. COOMBE.

Hon. Editor of the Journal of Animal Ecology: H. C. GILSON.

Hon. Editors of the Biological Flora: A. R. CLAPHAM, H. GODWIN, P. W. RICHARDS.

Council: the officers above together with: V. M. Conway (1957), J. B. Cragg (1957), M. W. Holdgate (1957), N. W. Moore (1957), H. B. Hynes (1958), O. W. Richards (1958), P. W. Richards (1958), F. H. Whitehead (1958), J. H. Barret (1959), E. M. Burrows (1959), D. E. Coombe (1959), J. F. Hope-Simpson (1959), P. F. Holmes (1960), R. E. Hughes (1960), T. T. Macan (1860), D. A. Webb (1960).

The year of retirement from Council is shown after each name.

123/1PC

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed : **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Dates should be in the form '1 Jan. 1956, 25 June' etc., not 'Jan. 1st. or with the month indicated by a figure. Text-figures are to be referred to as 'Fig. 1', etc. In the use of symbols, signs and abbreviations *British Standard 1991: Part I: 1954* should be followed, including the omission of all unnecessary full stops.

The *Journal's* conventions regarding cross-headings should be followed, but they should not be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form :

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7,** 303-4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals,* except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible ; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey ; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. OFFPRINTS. Authors are supplied with 50 offprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Offprints are sent out about a month after publication.